Forestry
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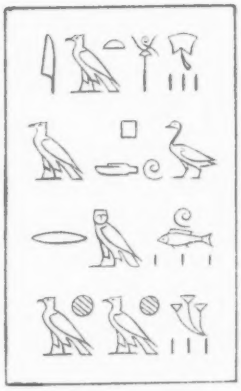
THE JOURNAL OF WILDLIFE MANAGEMENT



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The Journal of Wildlife Management is published four times a year in January, April, July, and October at 450 Ahnaip St., Menasha, Wisconsin, by The Wildlife Society.

Subscription $3.00 a year. Single copies 75¢. Entered as second class matter July 12, 1937, at the post office at Menasha, Wisconsin, under the Act of March 3, 1879.

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THE JOURNAL OF WILDLIFE MANAGEMENT

VOLUME 6 APRIL 1942 NUMBER 2

BOBWHITE FOODS AND CONSERVATION FARMING[1]

Verne E. Davison

There is widespread belief that the Southeast has an abundant supply of bobwhite foods as a result of the general use of legumes on cropland and because the natural vegetation embraces a wide variety of food plants. On the other hand the distribution, and the supply, of food is known to be poor in intensively cultivated sections.

Since 1935 the Soil Conservation Service has recognized an active wildlife improvement program as an inseparable part of a larger, more complete agricultural objective—the conservation of soil resources. While the term "wildlife" denotes all kinds of animals, the Service biologists have been primarily concerned with those species and problems most closely related to privately-owned farms. The bobwhite is but a single species, and therefore only a small portion of the farm biological problem, but a majority of the laymen in the Southeastern States think "birds," "partridges," "quail," or "bob-white," when wildlife is mentioned, thus reflecting a desire to see this thrilling game bird prosper. The appreciation by farmers of bobwhites adds to the sportsmen's demand for considerable emphasis on the improvement of bobwhite habitat.

When the objective is such development on several thousand farms a simple and concise set of recommendations is necessary. Most baffling is the fact that foods, whether sufficient in quantity or not, are usually neither dependably nor effectively interspersed with adequate shelter. Moreover, redistribution of food and cover on the average farm encounters many practical difficulties. For example, many biologists and game managers have been, and still are, recommending all of the following:

1. The planting of "food patches," including mixtures of cowpeas, beggarweeds, Japan clover, soybeans, Egyptian wheat, browntop millet, benne, buckwheat, sesbania, corn, wheat, and possibly other lespedezas, millets, sorghums, and small grains in an effort to supply variety.

2. The encouragement of native food plants such as partridge peas, beggarweeds, perennial bush clovers, ragweeds, butterfly peas, wild beans, vetch, Johnson grass, panic grasses, narrow-leaved buttonweed, and numerous others

[1] The author wishes to acknowledge gratefully the assistance of the field biologists of the Soil Conservation Service, the Mississippi State game wardens, the Georgia Division of Wildlife, and numerous Service employees and sportsmen who procured the material for us. Not the least of the value of this study was the opportunity it afforded to acquaint our own field men with the plants, their seeds, and their relation to agricultural practices.

either by protection against grazing and fire, or by controlled burning, or by disking to increase further the supply and variety of foods.

3. The establishment of hedges to break up large fields, and the planting of shrubs in gullies, fence rows, and even in woodland. These usually include blackberry, wild rose, redbud, American beautyberry, mulberry, wild plum, coralberry, privet, blueberry, wild grape, wild cherry, dogwood, oaks, and a number of others, to increase still further the variety of foods as well as to furnish adequate shelter.

4. Regulations and controls associated with laws, open seasons, bag limits, predators, diseases, surveys, formulas, and politics, and the restocking of lands by artificial means.

It is evident that these recommendations are entirely too complicated and too general for the agricultural producer. They are also largely unnecessary for the development of adequate food and shelter on most Southeastern farms. Many of the plants named are already abundant on some farms, but no one farm can afford to grow them all, and no one farmer can be expected even to know them.

The writer believed in 1937 that a more extensive study of bobwhite foods might aid in reducing the apparent confusion and in indicating more simple recommendations that would be adequate. The Food Habits Section of the Research Division of the Fish and Wildlife Service offered to assist in identifying any material that could not be determined by comparisons with samples in our more limited field reference collection. The methods of collecting, analyzing, recording, and summarizing the material were published in detail in the April 1940 issue of the JOURNAL OF WILDLIFE MANAGEMENT.

By using only the contents of crops, collected and examined in dry condition, by discarding gravel, chaff and other non-food items, and by ignoring minute quantities of food (less than 1 per cent by volume), usable data were accumulated from 5,889 bobwhites through three successive hunting seasons (November through February, 1937–38, 38–39, and 39–40).

PREVIOUS STUDIES

The most thorough studies up to 1937 had been made and published by Stoddard and Handley (1924–29) and Martin (1935).

Handley listed 105 "important plant foods of the bobwhite" of which 83 were "suitable for cultivation on quail preserves" as determined through field and laboratory studies of the Cooperative Quail Investigation. His findings were based on analyses of 1,659 stomachs over a 5-year period.

Martin listed and described briefly 46 "quail-food plants . . . in order of their use (preference) based on data derived from the analysis of stomach and crop contents of more than 2,000 bobwhites . . . in the Southeastern States. The data represent the findings of a number of investigators from 1900 to 1934 but the chief contribution was made by Stoddard and Handley . . . (1924–29) . . . in connection with the . . . quail investigation."

Gray (1938) published data derived from 440 bobwhite stomachs collected from the Blackbelt Soil Province of

Alabama from November 20 to February 20.

PRESENT STUDY

By using the contents of the crop alone, we eliminated the "inexactitudes of analysis for which only approximate accuracy (was) claimed" by Handley who considered the contents of either the gizzard or the crop, or both, as food of an individual. He recognized this as an "unavoidable error" because "hard portions of seeds . . . representing possibly several meals tend to collect in the gizzard." He apparently did not recognize then, the extent to which his results were distorted by study of the gizzards. Martin and Gray followed the same methods employed by Handley. Some of our conclusions differ from theirs solely because of this factor which is discussed in more detail in the April 1940 issue of the JOURNAL.

The percentages of food items are quite variable if only a small number of crops are recorded. Five groupings of 94 crops each from a collection of 471 crops were shown (Davison 1940) to vary considerably from each other and from the total average. By summarizing separately the odd and even numbers of a collection of 252 crops from Kemper County, Mississippi, in 1939–40, wide variations were noted in the same items, and 12 of the 46 items failed to show up in one or the other lots. We considered this factor so important that a summary of 1,016 crops was separated into the halves represented by the odd and even numbered crops and even then identical items varied up to 2.4 per cent of the total. However, no item of more than 0.2 of 1 per cent was missing from either half. This indicates that results from small collections are not sufficiently reliable, that items of less than 1 per cent are unlikely to be staple foods, and that all foods might well be grouped in classes of importance rather than in order of importance as determined by exact percentages.

The studies published by Stoddard, Martin, and Gray were based principally on winter foods taken from November through February. While Stoddard and Handley procured 56 crops in March and April, 122 from May through August, and 32 in September and October, it is evident that these numbers are hardly sufficient for final conclusions as to the relative importance of bobwhite foods through this 8-months' period. Field observations and these studies, however, must continue to guide the game manager's selection of summer food until someone can make more extensive examinations of bobwhite crop contents collected in spring, summer, and early fall.

The present investigation of bobwhite crops covers a wide section of the Southeast formerly little studied (Fig. 1). Local summaries for widely separated areas gave conclusive proof that certain foods taken freely in one community are quite unnecessary to the birds in another locality. As the studies increased in scope, one food after another was dropped from the list of indispensables, which was one of the results we sought. It finally became quite clear that there is no indispensable food item.

The application of game management in the field must be based on staple

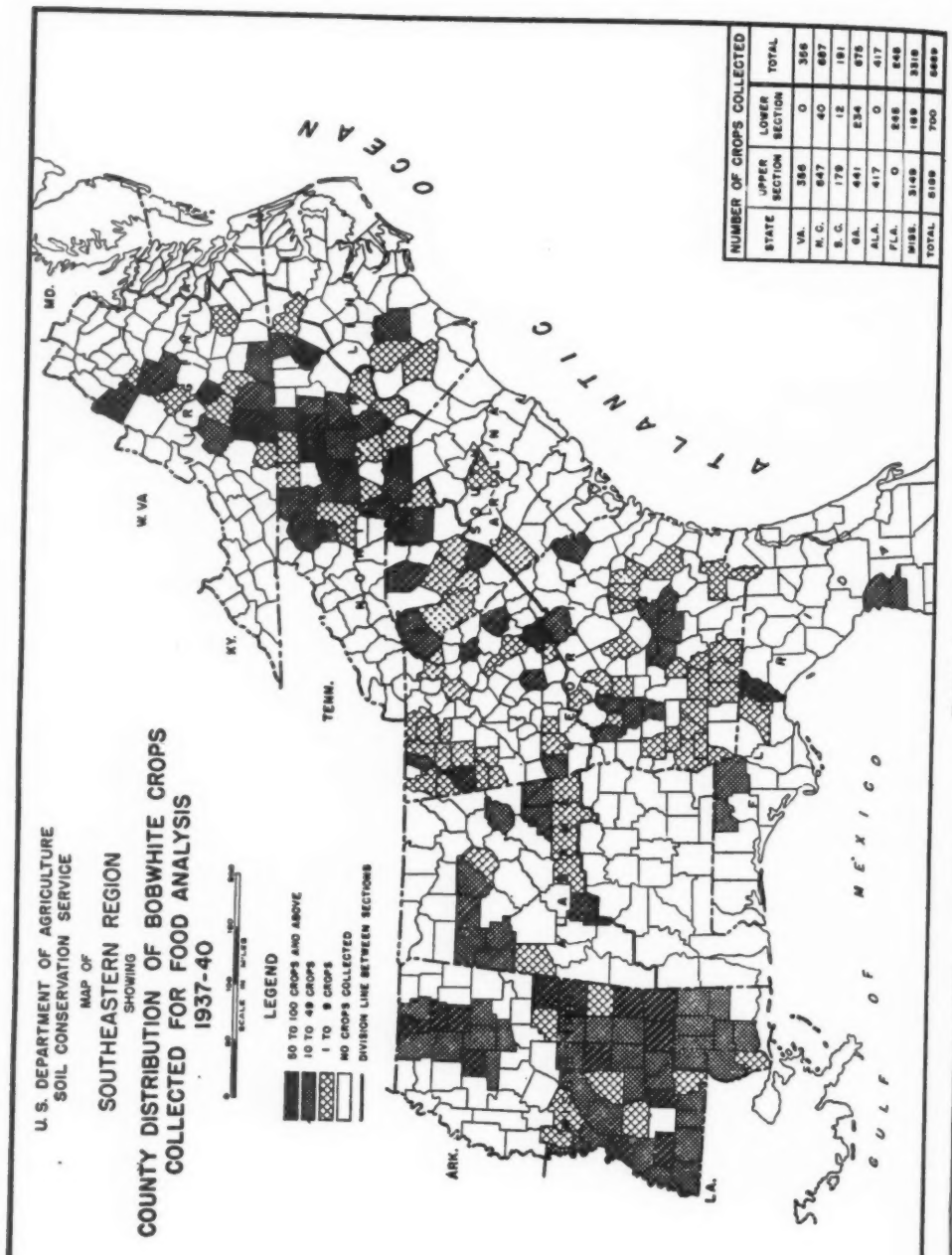
U. S. DEPARTMENT OF AGRICULTURE
SOIL CONSERVATION SERVICE
MAP OF
SOUTHEASTERN REGION
SHOWING
COUNTY DISTRIBUTION OF BOBWHITE CROPS
COLLECTED FOR FOOD ANALYSIS
1937-40
LEGEND
50 TO 100 CROPS AND ABOVE
10 TO 49 CROPS
1 TO 9 CROPS
NO CROPS COLLECTED
DIVISION LINE BETWEEN SECTIONS
ATLANTIC OCEAN
GULF OF MEXICO
MO.
W. VA.
KY.
TENN.
ARK.
LA.
NUMBER OF CROPS COLLECTED
STATE | UPPER SECTION | LOWER SECTION | TOTAL
VA. | 356 | 0 | 356
N. C. | 647 | 40 | 687
S. C. | 179 | 12 | 191
GA. | 441 | 234 | 675
ALA. | 417 | 0 | 417
FLA. | 0 | 848 | 848
MISS. | 3149 | 189 | 3338
TOTAL | 5189 | 700 | 6489

Figure 1

rather than preferred foods. Staple foods are those which will sustain life and health. Preferred foods are those which are taken by choice. To assure an ample supply of staple foods is difficult but to make preferred foods highly available on the farm is virtually impossible. The management of farm game should therefore be reduced to practical measures which will supply essential staples, and avoid the more expensive use of food patches catering to preferences.

With the present changing patterns of agriculture in mind, we studied single crops and combinations of crops to determine what influence the application of various soil conservation practices would have on bobwhite food requirements. Present trends in successful agriculture indicate that idle land (and the food and cover it produces) will soon be a thing of the past in the Southeast, in fact, in the nation. Every practical soil conservation measure must eventually be applied to all profitable farm enterprises. Only incidental foods will then be available for game conservation. In this connection a significant fact is unheeded all too often by the game technician and the wildlife instructor; foods (or shelter) that must be produced primarily for wildlife lack sufficient economic justification to overcome the average farmer's inertia or his financial incapacity; conversely, all the foods (and shelter) that can be produced for wildlife as a by-product of profitable agriculture are welcomed by the average farmer because they are economically produced. These considerations lead to the conclusion that every effort should be made to replace the foods of the now disappearing idle lands and those usually recommended for an annual food patch with others that can be produced more dependably or more economically.

Very little is available in the literature concerning the farm implications of bobwhite foods. This is due perhaps to insufficiency of data, lack of agricultural knowledge, or to some other factor that has prevented the reduction of foods and farming to a common denominator. With reference to statewide developments for quail, Stoddard wrote, "measures to insure success must be few and simple." Bode stated, "If we cannot show how wildlife management can fit into other regularly accepted forms of land use and land practice . . . we are not going to get very far with wildlife management. The one big difficulty . . . is that you cannot tell them (farmers) what to do . . . " Seth Gordon expressed it by saying "Unfortunately we do know a lot of things that need to be done but we have not been able to set up machinery to apply them or get them to those who are living on the land and are (therefore) in the best position to apply them." In other words the recommended food patches and other special features of management have not returned sufficient benefits to tempt practical agriculturists to adopt them.

For the present study, quail crops were collected from the 195 counties that are shaded on the accompanying map of the Southeastern States (Fig. 1). In the discussion, the 5,889 crops assembled have been divided into two groups according to the areas indicated on the map by the line dividing the

region into upper and lower sections. The upper section includes the soil provinces known as the Piedmont Plateau, Limestone Valleys, Blackbelt, upper Coastal Plain, and the Loessal Belt. The lower section includes the middle and lower Coastal Plain. The most thorough coverage of a single area, northern Mississippi, for all three years yielded 1,835 crops. A report on these was published by Johnson in 1940. Ruggles (1940) gave the relative importance of Blackbelt foods as revealed by study of 225 crops collected in Perry County, Alabama during the 1938–39 season.

The following discussion applies only to the 5,189 crops collected in the upper section since the 700 from the lower section are deemed too few in number for definite conclusions.

Table 1 lists 130 groups, chiefly plants, which were found to contribute 1 per cent or more of the contents of at least 1 of the crops. These food sources have been separated into 5 groups according to their importance. Average volumes of food gleaned from them are given for the 3 years and for each year separately.

Group I embraces but 6 plants the products of which occur frequently and in large proportion in crops collected over wide areas. This group may safely be further reduced to two for any one farm or single locality comprising the oaks and one of the following: annual lespedezas, cowpeas, soybeans, partridge peas, or beggarticks, whichever can be grown most economically.

Annual lespedezas grow well throughout this section. Korean lespedeza (*L. stipulacea*) sometimes called Japan clover, was introduced about 20 years ago and has become a common soil-building and annual hay crop through much of Virginia and both Carolinas, and is rapidly spreading through Georgia, Alabama, and Mississippi. This plant supplied 71 per cent of the foods taken by 62 bobwhites collected in central Virginia in 1938–39, and common lespedeza (*L. striata*) and Korean together furnished 61 per cent of the food in 602 crops collected from Virginia and North Carolina the same year.

On the other hand, collections from several localities in Mississippi, Alabama, and Georgia, showed cowpeas or soybeans to be taken almost to the exclusion of annual lespedezas. In Perry County, Alabama, partridge peas (*Chamaecrista* spp.) reached their highest percentage (21.8 per cent).

Group II comprises 11 items, including insects and greens which usually need not be considered in game management programs as both as a rule will be present in sufficient quantity naturally. (Greens may have been given a rank slightly lower than they deserve owing to the dry method of handling. They are, however, the only item that is materially reduced in volume by drying and which thus becomes difficult to measure with accuracy.) With the single exception of the perennial bush clovers, the other 9 plants in this group are generally valuable sources of food and may be available in fair quantities under normal farm operations. On the other hand, the absence of any one or all of them would not be likely to jeopardize the winter food supply of bobwhites if acorns and legumes were available in sufficient quantity.

TABLE 1

3-YEAR SUMMARY OF BOBWHITE FOODS TAKEN IN UPPER SECTION OF THE SOUTHEAST

Food Source	Number of Crops			
	5,189	871	1,909	2,399
	3-Year Average	1937–38	1938–39	1939–40
Group I				
Annual lespedezas (L. striata & L. stipulacea)	33.5	36.7	36.7	29.6
Oaks (Quercus spp.)	13.4	19.0	11.6	12.8
Cowpea (Vigna sinense)	7.1	5.7	7.8	7.0
Soybean (Soja max)	5.1	4.3	6.6	4.1
Beggarticks (perennial Desmodium spp.)	5.0	5.2	2.3	7.0
Partridge peas (Chamaecrista spp.)	4.3	2.3	5.5	4.1
Group II				
Ragweed (Ambrosia elatior)	3.0	0.3	4.3	2.9
Bull grass (Paspalum boscianum)	2.7	0.4	1.5	4.6
Pines (Pinus spp. except P. palustris)	2.6	0.6	0.5	4.9
Milk peas (Galactia spp.)	1.8	1.8	2.0	1.6
Bush clovers (perennial Lespedeza spp.)	1.6	3.4	1.5	1.0
Sweetgum (Liquidambar styraciflua)	1.5	0.6	0.7	2.4
Insects & other animals	1.5	1.2	1.5	1.6
Greens	1.3	1.3	0.8	1.8
Corn (Zea mays)	1.3	0.6	1.5	1.4
Flowering dogwood (Cornus florida)	1.1	3.4	1.0	0.2
Wheat (Triticum)	1.0	0.3	0.7	1.4
Group III				
Small wild bean (Strophostyles umbellata)	0.8	T[1]	1.3	0.6
Pecans (Hicoria)	0.7	1.2	T	1.1
Sorghum vulgare	0.7	0.6	0.9	0.6
Ground nut (Apios americana)	0.7		1.6	0.2
Sumacs (Rhus glabra & R. copallina)	0.6	0.7	0.5	0.6
Ashes (Fraxinus spp.)	0.5	0.4	T	1.0
Butterfly pea (Centrosema virginianum)	0.5	0.1	0.7	0.5
Goat weed (Croton capitatus)	0.5	2.0	0.2	0.3
Honeysuckle (Lonicera japonica)	0.5	0.1	0.7	0.5
Longleaf pine (Pinus palustris)	0.4			0.8
Black gums (Nyssa spp.)	0.4	2.1	T	T
Jewel weeds (Impatiens spp.)	0.4	0.4	0.5	0.2
Johnson grass (Sorghum halepense)	0.4	T	0.9	0.1
Pink bean (Strophostyles helvola)	0.3		0.4	0.4
Crab grass (Digitaria sanguinalis)	0.3	0.1	0.3	0.4
Black locust (Robinia pseudoacacia)	0.3	T	0.4	0.3
Vetches (Vicia spp.)	0.3	0.1	0.4	0.2
Hog peanut (Amphicarpa bracteata)	0.3	T	0.4	0.2
Group IV				
Black cherry (Prunus serotina)	0.2	0.6	0.1	0.2
Crab grasses (Digitaria spp.)	0.2		0.2	0.3
Poison ivy (Rhus radicans)	0.2	T	0.3	0.2
Sesbania (Sesbania exaltata)	0.2		T	0.4
Panic grasses (Panicum spp.)	0.2	0.1	0.1	0.3
Sparkleberry (Vaccinium arboreum)	0.2	0.7	T	0.1
Dayflowers (Commelina spp.)	0.1		0.2	0.2
Rye (Secale cereale)	0.1	0.2	0.2	T

[1] T=trace

TABLE 1 (*Continued*)

Food Source	Number of Crops			
	5,189	871	1,909	2,399
	3-Year Average	1937–38	1938–39	1939–40
Osage orange (Maclura pomifera)	0.1		0.4	
Grapes (Vitis spp.)	0.1	0.1	0.1	0.2
Sassafras (Sassafras albidum)	0.1		0.3	T
Yellow foxtail (Setaria lutescens)	0.1	T	T	0.2
Pink bean (Strophostyles pauciflora)	0.1		T	0.2
Marsh elder (Iva ciliata)	0.1		T	0.2
Paspalum spp.	0.1	0.3	0.1	0.1
Lespedeza sericea	0.1	T	0.3	
Maples (Acer spp.)	0.1	0.1	0.1	T
Rough buttonweed (Diodia teres)	0.1	0.1	T	0.1
Congo-root (Psoralea psoralioides)	0.1	0.2	T	0.1
Spangle grass (Uniola)	0.1		T	0.2
Blue curls (Trichostema dichotomum)	0.1	0.1	0.1	0.1
Rhynchosia spp.	0.1	0.1	0.1	0.1
Catalpa spp.	0.1		0.1	T
Maypop (Passiflora incarnata)	0.1	T	0.1	T
Oats (Avena sativa)	0.1		0.1	0.1
Polygonaceae	0.1	T	0.1	T
Beech (Fagus grandiflora)	0.1	0.3		
Group V				
Acalypha virginica	T		T	
Acmispon helleri	T		0.1	T
Agrostemma githago	T		0.1	T
Albizzia julibrissin	T		T	
Amaranthus spp.	T	T		
Ambrosia trifida	T		T	
Amorpha fruticosa	T		T	
Ampelopsis arborea	T		T	
Arachis hypogaea	T		T	
Aronia arbutifolia	T			T
Barbarea verna	T		T	
Benzoin aestivale	T		T	T
Betula nigra	T			T
Bidens spp.	T	T	T	0.1
Bignonia radicans	T	T	T	T
Callicarpa americana	T		0.1	
Carpinus caroliniana	T		T	T
Ceanothus americanus	T		0.1	T
Celtis spp.	T			T
Cercis canadensis	T			T
Citrullus citrullus	T		T	
Clitoria mariana	T		T	
Cornus asperifolia	T			T
Crataegus spp.	T	0.1		
Crotalaria spp.	T		T	T
Croton glandulosus	T		T	
Cyperus spp.	T		T	T
Dactyloctenium aegyptium	T		0.1	T
Desmanthus illinoensis	T		T	
Desmodium tortuosum	T			T
Dioclea multiflora	T		T	
Diospyros virginiana	T	0.1		
Euphorbiaceae	T		T	
Geranium carolinianum	T			T

TABLE 1 (*Continued*)

Food Source	Number of Crops			
	5,189	871	1,909	2,399
	3-Year Average	1937–38	1938–39	1939–40
Helianthus spp.	T		T	T
Ilex glabra	T		T	
Ipomoea spp.	T		T	
Juniperus virginiana	T		T	
Lathyrus spp.	T			T
Liliaceae	T		T	
Lithospermum spp.	T		T	
Magnolia spp.	T			T
Mentha spp.	T		T	
Myrica caroliniana	T		T	T
Myrica cerifera	T			T
Ostrya virginiana	T	0.3		
Panicum ramosum	T		T	
Parthenocissus quinquefolia	T		T	0.1
Persea borbonia	T		T	T
Phaethusa virginica	T		T	
Phaseolus vulgaris	T		0.1	T
Physalis spp.	T		T	
Phytolacca americana	T	T	0.1	T
Richardia scabra	T		T	T
Rosa spp.	T		T	T
Scleria spp.	T		0.1	T
Setaria italica	T		T	
Sida spinosa	T		T	T
Smilax spp.	T	0.1		T
Solanum sp.	T			T
Stylosanthes biflora	T			T
Symphoricarpos orbiculatus	T		T	
Tephrosia spp.	T		0.1	T
Teucrium canadense	T		T	T
Thyella tamnifolia	T		0.1	T
Trifolium spp.	T			T
Viburnum spp.	T		T	T
Zornia bracteata	T		0.1	T
Unidentified	0.3	1.6	0.2	0.1
	100.0	100.0	100.0	100.0

Group III includes 18 food plants which supply considerable food under certain circumstances. Sumac and honeysuckle are probably most sought when snow storms occur. This would not be reflected in the present study as little hunting of bobwhites is done when snow lies on the ground.

Group IV includes 27 food plants that were represented occasionally in limited quantites or rarely in substantial amounts. The correctness of the assignment of *Lespedeza seraice* to this group should be further investigated as this plant was not available to many birds taken for this study.

Group V includes 68 plants listed alphabetically that may be regarded as inconsequential producers of bobwhite foods in winter since their representations were infrequent or in very small amounts. Nevertheless, many of these

species were abundantly available.

How may these foods be supplied incidentally to ordinary farming operations? The following discussion by land-use classes is based on the results of this food study and on practical farm economics.

WOODLANDS AND IDLE AREAS

Within woodlands are large numbers of oak (Group I), pine (II), sweet gum (II), flowering dogwood (II), black gum (III), and some ash (III), hickory (III), maple (IV), and beech (IV). In post patches, black locust (III), osage orange (IV), and catalpa (IV) may be produced where fence posts are purposely raised.

Along stream banks and in moist spots in woodlands, perennial beggarticks (I), butterfly pea (III), jewel weed (III), hog peanut (III), and Psoralea (IV) may continue to supply considerable food, but we know of no management that should be undertaken to increase them. In the more open, drier woodland situations and on idle fields, still other beggarticks (I), partridge pea (I), bush clover (II), and milk pea (II) are frequently abundant. As pointed out by Stoddard, however, a satisfactory supply of these legumes on such sites can be assured only by controlled burning at intervals. The value of light burning has not been widely demonstrated in the upper section of the Southeast and the practice is primarily applicable to the larger land holdings for game preserves rather than to average farm lands to which this paper is largely devoted.

Both woodland and idle areas have been permitted to burn over frequently with little or no control and on them have volunteered many native leguminous food plants. This present crop study indicates, however, that ample foods can be provided to replace those lost as a result of the discontinuance of burning provided the woodland areas are small and interspersed with a larger acreage of cropland. Fire might be used to the advantage of bobwhites in relatively small woodlands to encourage quail production but there are more basic practices which are needed first on the ordinary farm.

There is no permanent place in this rather intensively farmed section for idle areas such as are now scattered through it. Idle land results from ill-planned, unstable, or wasteful practices that are on their way out.

WILDLIFE LAND

In the woodland border may be developed, by selective thinning, flowering dogwood (II), honeysuckle (III), sumac (III), black cherry (IV), sparkleberry (IV), grape (IV), sassafras (IV), and summer fruits such as blackberries, dewberries, and plums. Practical farm management and economic farm-forestry are sufficient reasons for protecting and encouraging an adequate supply of all these woody plants in the sites to which they are adapted. To recognize their wildlife use is to add incentive for their care and to increase appreciation of their usefulness.

The same shrubs that fit woodland borders are also needed for stream bank protection and can be managed in well kept hedges. On the other hand the farmer usually will not accept recommendations to plant plums, blackber-

ries, and other root-suckering shrubs in hedges between cultivated fields.

We have experimented with the annual partridge peas (I) and the native perennial lespedezas (II) but have been unable to determine a practice by which they may be satisfactorily produced under ordinary farm conditions. In fact, the importance of the native lespedezas appears to have been exaggerated by gizzard analyses and there seems to be no need for partridge peas (I) where annual lespedezas (I) may be substituted. On the other hand the introduced perennial *Lespedeza sericea* (IV) is exceptionally useful on field borders where erosion control is badly needed. Its value as cover at this strategic location is unquestionable and its utility as an emergency food seems reasonable.

CROP LAND

The possibilities of producing more food for wildlife and assuring its better distribution on crop land are indeed promising. Annual lespedezas (I), cowpeas (I), soybeans (I), corn (II), wheat (II), vetch (III), rye (IV), oats (IV), and *Lespedeza sericea* (IV) are staple crops of the Southeast. Accompanying these crops are the following weeds that may be expected to continue to prosper with southern agriculture: ragweed (II), bullgrass (II), crabgrass (III), dayflower (IV), foxtail (IV), and blue curls (IV). An adequate soil-conservation program usually includes the planting of an annual lespedeza and either wheat, rye, or oats in rotation with cotton or corn on sloping fields. Cowpeas or soybeans are commonly interplanted with corn. The practice of growing cowpeas and soybeans alone for hay has prevailed in some sections but it is on the wane because it neither conserves the soil nor provides cheap feed. The substitution of annual lespedezas for cowpeas and soybeans is definitely beneficial to bobwhites as the food supplied by the lespedeza is not so easily and quickly gleaned. A still more encouraging trend is that toward perennial hays as kudzu (*Pueraria thunbergiana*) and *Lespedeza sericea* on land not good enough for row crops. This allows the annual lespedeza to remain on the land and to return to the soil for the benefit of the row crops which follow sufficient improvement. Ragweed seems assured the first year with lespedeza following small grain in a 3- or 4-year rotation system.

More important to bobwhite welfare than any other single factor appears to be the practice of strip cropping, that is, of growing all crops of a rotation in adjoining strips within each field. Farmers are often reluctant to adopt farming by strips but those who are interested in wildlife should not overlook the positive benefits of this system. To wildlife, strip farming brings security by supplying legumes, waste grain, stubble, and weeds and greens adjacent to the permanent shelter every year, whereas the usual practice has supplied abundant food every second, third, or fourth year and none at all during one or more years in between. Dambach and Good (1940), and Edminster (unpublished) have found increased numbers of birds in strip-cropped fields.

PASTURES

The improvement of pastures should indirectly benefit wildlife by removing

livestock from the crop fields and thus sparing ragweed, legumes, and other food plants. Within the pasture some benefit can be expected from the inclusion of common lespedeza in pasture mixtures. It hugs the ground so closely as in part to escape destruction. A campaign to increase livestock in the Southeast will probably offset advantages gained by improving pastures because livestock doubtless is one of the most destructive influences operating to reduce bobwhite food and shelter.

The supply of goat-weed (III) seed will be reduced by pasture management since it is usually most abundant on over-grazed areas. An increase in small grain acreage may offset this reduction as the plant, like ragweed (II), grows well following small grain.

In summarizing, a few simple practices are recommended:

1. Grow annual lespedezas in strips in the crop-rotation system. Small grains included in the rotation will increase further the food supply of waste grain and following weeds. Cowpeas and soybeans are valuable when grown with corn. Bullgrass and crabgrass may be left at the last cultivation. All are thus economically produced and distributed throughout the farm as by-products of a definite crop-rotation system.

2. The mast of oaks, gums, pines, hickories, and ashes can be provided in woodland, which should be protected from grazing.

3. Wildlife borders (Davison, 1941) should be developed on the edges of fields. *Lespedeza sericea* is suitable for the herbaceous portion and native shrubs are dependable for the heavier cover. Though shrubs are normally of little value in providing winter food for bobwhites, honeysuckle, dogwood, and sumac are doubtless useful in emergencies. Blackberries and other summer fruits are also desirable. Protect shrubs in marshy areas, on stream banks, in fence rows, on rocky outcrops, and other small uncultivatable steep slopes, but manage them so as to keep them low and compact and prevent them from spreading into adjoining cropland.

4. Plant enough kudzu or sericea to supply the hay requirements of the farm livestock and at the same time assure availability of seed from annual legumes which should be returned to the soil to increase its humus content.

Until full advantage has been taken of these simple principles for producing food and shelter to supply the winter needs of the bobwhite, more intensive measures can hardly be justified. These measures of wildlife management are being accepted by farmers and are being advocated by agricultural workers who have not responded to pleas for less practical measures. If the shelter and foods now supplied by idle land are to be replaced when idle land no longer exists, it must be by improved yet practicable farm management measures for game conservation.

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A THREE-YEAR TRIAL WITH A FEED PATCH FOR SONGBIRDS

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In 1938 a trial feed patch for songbirds was prepared at Pleasant Valley Bird and Wildflower Sanctuary in Lenox, Massachusetts, by tilling a 1½ acre plot of old field and sowing it with a mixture of selected seeds. Partially successful in 1938, the experiment was repeated—with minor modifications and improved results—by reseeding the same area in 1939 and 1940. The venture had two motives: (1) To improve feeding conditions for the summer resident and migrant fringillids already common on the Sanctuary, and (2) to attract a number of seed-eating birds which, for reasons not altogether clear, have always been absent or scarce. The feed patch functioned admirably in meeting the first need, but failed in the second.

Feed patches for wildlife have been used in other regions, frequently by conservation agencies interested in food and cover improvement for game birds, more rarely by persons primarily concerned with helping songbirds. In fact one of the shortcomings of feed patches in game management projects has been the early harvesting of the grain by blackbirds and sparrows. The Williamston Cooperative Game Management Project, after several years trial, recommended a seed mixture containing 17 selected grains for use in southern Michigan (English, 1935); but the Vermont Fish and Game Service using a similar mixture found that many of these grains did not mature well in that State. Bump (1936) reported considerable success with various seeds in the scrub oak area of Long Island, but J. Paul Miller (1936) indicated general failure for ten trial plots on barren forest soils in the Pillsbury, New Hampshire, Game Management Project. For the Kellogg Bird Sanctuary in Michigan, Durward Allen (1938) reported in some detail on two winters' observations of experimental plots on various soils.

The outstanding shortcoming of all feed patches has been the failure of any grain (except possibly corn for quail and pheasants) to provide inexhaustible supplies through the critical winter months, especially in northern regions where heavy snow prematurely buries the plants. This paper contributes nothing toward solving that difficulty. It merely records observations on the favorable and unfavorable features of a three-year trial plot for seed-eating passerine birds.

Choice of Seeds

In view of the failure of a large part of the many-seed mixture to reach maturity in Vermont, it seemed best in plantings in the somewhat similar Berkshire region to use only a few grains of proved hardiness. Consequently sowings were limited to millet, sunflower, buckwheat, and hemp, with the more or less incidental addition, in 1940, of small quantities of oats, barley, and corn. Corn, highly approved for

game birds, was omitted because there were none of these birds on the area and because of the unwelcome prospect of attracting too many crows.

Hemp would be a desirable constituent of feed patches in view of the capacity of its stiff stems to withstand winter storms, and of the fact that its seeds are favorites with birds. But the hemp seed used, in spite of assurances of viability from the dealer, failed to germinate, the reason becoming readily apparent when it was learned that hemp seed has to be sterilized in accordance with strict Federal regulations to prevent germination and possible subsequent use of the plant in the manufacture of the habit-forming drug, marihuana.

Buckwheat, though a good source of food for grouse, quail, and pheasants, was of minor value for songbirds. To some extent it was picked open in its early stages before the other seeds matured, and it had additional value from its soil-improving (nitrogen-fixing) qualities, and as a source of nectar for honey-bees.

Sunflowers were an attractive and useful addition to the seed plot, although they did not mature seeds to full capacity in 1938 and 1940. Fertilizer, little used because of its high cost, was applied in 1939, and together with the more favorable season greatly benefited the sunflower production. The seeds were harvested mainly by goldfinches, chickadees, and bluejays in September and October.

Millet was the mainstay of the majority of the birds frequenting the feed patch. It matured well during all three seasons, under climatic conditions varying from a summer of drought to one of excessive rain. Fertilizer improved the yield, but lack of it did not prevent fair production and ripening. Perhaps fortunately, the seed used was impure, including both *Setaria italica* and *Echinochloa frumentacea*, as well as a generous sprinkling of seeds of weeds. Maturing of the millets roughly coincided with the fall migration of seed-eating fringillids.

Discussion and Conclusions

Although there was a marked concentration of birds in the feed patch when the grain was available, the number of species regularly resorting to it for food was somewhat disappointing. About 15 species, mostly seed-eating fringillids, used the patch regularly for fall feeding grounds. Numbers of others, more than 60 species in all, were attracted for a variety of reasons, perhaps in no small part because of the gregarious tendencies of birds in migration. Warblers, vireos, catbirds, wrens, kinglets, and other insectivorous species were to be found about the tree-and-shrub-bordered outskirts of the field in September and early October, some of them frequently entering the grainfield.

One disappointing feature of the seed patch was its failure to lure certain field birds whose scarcity here had been assumed to be due, at least in large part, to the lack of farming which ordinarily provides both the habitat and the food supply for meadow birds. In twelve years of observations, neither the northern nor the prairie horned larks had ever been recorded, snow buntings were limited to rare winter visitations, and longspurs were unknown. Siskins, found feeding on millet as early as August in Vermont, have not been seen at the

Sanctuary in the past four years, and redpolls have come only during periods when the feed was covered by snow. The vesper sparrow appeared at the feed patch only once and then did not stay. Apparently these birds, all chiefly seed-eaters, especially in the fall and winter, and said to be fond of millet (Forbush, 1925, 1929), have not found the feed patch. Bobolinks, meadowlarks, and pipits, though primarily insectivorous, at least in New England, might conceivably have been attracted by the tilling of the land, but none came.

Failure of crows, starlings, blackbirds, and house sparrows to find the abundant food supply in the patch was probably a fortunate circumstance. Starlings were frequent passers-by, but seldom stopped. Redwings and bronzed grackles were summer residents at the Beaver Ponds within half a mile, but they left their nesting grounds in late summer and seldom reappeared till the following spring. Migrating flocks of rusty blackbirds, frequent especially in spring, have not visited the grainfield. Neither summer resident, nor migrant, crows have shown any interest in the plot. House sparrows, fortunately, are rare visitors at any time of year. An invasion of the seed patch by hordes of any of these species would make short work of it.

An outstanding shortcoming of all seed-patches is the brief period of availability of food. The grain is not ready until late August (if planted earlier it would mature too early) and here it has been exhausted before the end of November, at the beginning of the critical winter period when from the standpoint of food shortage it is most needed. Late-arriving tree sparrows and fox sparrows and late-lingering juncos usually made rather indifferent use of the patch. By December, even with the light snow cover prevailing in 1939 and 1940, the area was largely deserted. Winter finches have never appeared on the plot and presumably would find it of little value if they did. Seed-eaters are not a prominent part of the winter avifauna of the Berkshires, in fact most of them are of rather rare and unpredictable occurrence; those that do come depend upon birch and alder catkins rather than upon weed seeds.

Examination of carefully kept arrival and departure dates at the Sanctuary over a period of twelve years reveal little if any change in dates of migration that could be attributed to the presence of the feed patch, although there were a few cases of altered local distribution in the fall. Goldfinches, with their characteristic itch to be on the move, practically deserted the patch in mid-September just before their favorite sunflower seeds were fully ripened. Indigo buntings, Lincoln sparrows, and the bulk of the song sparrow and whitethroat population disappeared either before the feed was past its peak or at least long before it was exhausted.

The most apparent local distributional change was among indigo buntings. Although unfailing summer residents at the Sanctuary, there were no fall records for the species until 1939 and 1940 when they remained in the feed patch in considerable numbers into early October. Similarly, swamp sparrows and field sparrows, though common summer residents at the Sanctu-

ary, have been rare or wanting in fall according to past records, until the feed patch, to all appearances, caused them to linger to late dates. As in the case of the buntings, however, this does not necessarily indicate a postponement of migration, but may rather be a local distributional change in response to unusual availability of food.

Annotated List of Species

Following is a systematically arranged account of the birds that made more than incidental use of the patch during the three seasons of observation:

Ring-necked Pheasant (*Phasianus colchicus torquatus*)

A pair of pen-reared ring-necks were liberated in the feed patch in the fall of 1938, but they soon disappeared. In 1940, however, a wild cock from an unknown source appeared and virtually lived in the feed patch from October 13 to November 18.

Blue Jay (*Cyanocitta c. cristata*)

Blue jays in numbers up to a dozen perched on the sunflower heads and pulled out the seeds, persisting in this occupation day after day until the seeds were gone.

Black-capped Chickadee (*Penthestes a. atricapillus*)

Chickadees joined with the blue jays in harvesting the sunflower crop, their superior numbers compensating for their smaller individual capacity. Blue jays either swallowed the seeds entire on the spot or carried off a whole cropful at each trip, whereas the chickadees took one seed at a time to a nearby tree or bush to extract the kernel. The chickadees resorting to the area were largely permanent resident individuals and young birds, emerging from the woods before the arrival of the winter residents. Because of exhaustion, the seed patch was of little or no use to wintering individuals.

Northern Yellowthroat (*Geothlypis trichas brachidactyla*)

Unlike other insectivorous species, northern yellowthroats made more than occasional use of the feed patch, being summer residents in the grain and along the shrubby borders of the plot. Possibly the plantings increased their insect food, or the attraction may have been cover. One was seen in the vicinity on October 26 in 1939, Berkshire's latest record for this species.

Indigo Bunting (*Passerina cyanea*)

Although one to several pairs of indigo buntings have been unfailing Sanctuary summer residents in the past twelve years there were no September or October records for the species until 1939 and 1940, when a dozen or more individuals frequented the feed patch throughout September and into early October, the last observation being on the 7th. In this case the presence of the feed patch appears to have influenced local behavior of a species, for although the prevalence of buntings in 1939 and 1940 may be in part correlated with their regional increase during those years, it seems equally probable that the presence of adequate foraging grounds prevented their deserting the Sanctuary in July and August as they had done during the ten previous years.

Purple Finch (*Carpodacus p. purpureus*)

It was somewhat unexpected that purple finches made little use of the feed patch. They were often noted passing over the plot throughout the period of the availability of their favorite sunflower seeds, but they seldom paused more than long enough to survey the field from the tree tops and only rarely in the three years did they actually descend into the patch

Eastern Goldfinch (*Spinus t. tristis*)

Goldfinches were among the first occupants of the patch, frequenting it in some numbers in July and early August before the grains were mature and increasing to large flocks in late August and early September. They seemed most abundant in 1938, a comparatively poor sunflower year, feeding extensively on millet and weed seeds, but deserted the area by mid-September. They behaved somewhat similarly in 1939 and 1940; in the latter year a few lingered, however, into November.

Red-eyed Towhee (*Pipilo e. erythrophthalmus*)

One pair of towhees is usually resident in summer in an area adjacent to the feed patch, but in the fall a dozen or so individuals could usually be found in the plot. In 1940 a much belated towhee was found there from November 10 to 18, the Sanctuary's latest record by nearly a month.

Slate-colored Junco (*Junco h. hyemalis*)

Juncos arrived in the feed patch at very variable dates: early September, 1938, late September, 1939, and early October in 1940. They came in small numbers at first, increasing to hundreds, at least in 1939 and 1940, by mid-October and lingering well into November. Juncos do not winter at the Sanctuary and only stragglers were noted later than November 17, the latest date for a flock of any size. They were not particularly dependent on the feed patch, using it very little in 1938, and though visiting it in large flocks during the succeeding two years, they gave equal attention to the lawn, grassy meadows, and woods.

Tree Sparrow (*Spizella a. arborea*)

Tree sparrows arrive at the Sanctuary in great numbers in late October or early November. In 1938 the depleted state of the feed patch at the time of their arrival apparently rendered it practically useless for them, but in 1939 and 1940 they resorted to it in considerable numbers, together with fox sparrows and juncos administering the finishing touches to the fast-disappearing grains. During all three years, however, the bulk passed on, as usual, before the end of November. Eight to fourteen tree sparrows have wintered at the Sanctuary during the past four years, but they rarely used the feed patch.

Field Sparrow (*Spizella p. pusilla*)

This species is another example of a summer resident bird rarely staying at the Sanctuary in the fall until the feed patch apparently induced them to do so. The number of individuals was small, but a few were present almost daily in September and October, linger-

ing to the here unprecedented late date of November 2, in 1939.

White-crowned Sparrow (*Zonotrichia l. leucophrys*)

This species has been on the decline at the Sanctuary in the fall during the past four years and their sojourn shortened in spite of the feed patch. The peak year was in 1937 before the feed patch was started. In 1939 and 1940 appeared belatedly (on October 5) a few individuals that lingered only a few days. Though usually to be found in the feed patch during their short sojourn here, they nevertheless left when the seeds were still abundant.

White-throated Sparrow (*Zonotrichia albicollis*)

A few forerunners, presumably local summer residents, in early September usually preceded the hordes of white-throats that came a little later. Before the close of the month many hundreds, it not thousands, of white-throats were present. This peak remained fairly constant until mid-October witnessed a sharp decline, leaving only occasional strays in the first half of November. By far the most abundant occupants of the feed patch, their metallic alarm notes and frequent snatches of song could be heard from a considerable distance, and when disturbed they rose from the field with a loud whir of wings. They made heavy inroads on the seed supply, but, rather unexpectedly, the bulk of them began to pass on considerably in advance of the depletion of the feed. From previous departure dates at the Sanctuary there is no evidence that the great quantity of readily available food in any way halted their main southward march, for they seemed to come and go on about their customary schedule. Their abundance in the patch was apparently merely a local concentration in response to good feeding conditions, which they took advantage of without serious interruption to their inherent rhythm of migration.

Fox Sparrow (*Passerella i. iliaca*)

The crest of the fox sparrow fall migration in the Berkshires comes in late October and early November with forerunners and stragglers considerably before and after those dates. In 1938 they were too late for much use of the feed patch, but in 1939 and 1940, with the better yield and duration of the grains, they helped consume the already somewhat depleted crop.

Lincoln's Sparrow (*Melospiza l. lincolni*)

This sparrow, although more numerous in the fall than in the spring, is far from common and is often missed by local observers. It seems some tribute to the usefulness of the feed patch, therefore, that this elusive bird was to be found there in small numbers almost daily from mid-September or later into early October. Disappointingly, however, no grasshopper nor Henslow's sparrows and none of the James Bay sharp-tails have been found in the feed patch.

Swamp Sparrow (*Melospiza georgiana*)

This summer resident species, like the field sparrow, was only irregularly recorded in the fall before the establish-

ment of the feed patch; thereafter they became daily patrons, lingering to the unprecedented late dates of November 2, in 1939 and November 1, in 1940. Here again is illustrated a local distributional change, though probably not actual postponement of migration.

Song Sparrow (*Melospiza m. melodia*)

In spite of the superior numbers of white-throats, song sparrows probably derived greater benefit from the plot than any other species. A few pairs were resident in and around the tract from the first, foraging over the cultivated ground in spring, using the growing grain for cover and possibly belated nesting sites in summer, and feeding on the mature seeds in the fall. After the breeding season, additional adults and young moved into the area, presumably from nearby summer territories, a number further augmented by migrants through late September and most of October. By the end of October they had largely disappeared, only a few belated birds tarrying into November.

SUMMARY

1. During three years (1938–1940 inclusive) a trial feed patch for songbirds has been in use at the Pleasant Valley Bird and Wildflower Sanctuary, Lenox, Massachusetts.

2. The purpose of the seed plot was to improve feeding conditions for the birds already present, and to attract, if possible, a number of field species that have heretofore been absent or scarce at the Sanctuary.

3. Choice of seeds was limited to a few hardy grains—millets, hemp, sunflower, and buckwheat—because of the failure of items in a many-seed mixture to reach maturity in nearby Vermont. The use of hemp had to be discontinued because of a Federal seed sterilization requirement.

4. A heavy concentration of seed-eating fringillids frequented the patch from mid-September through October, with smaller numbers using it before and after this period. Only fifteen species, however, used the patch regularly for feeding grounds, although about 45 others visited it more or less incidentally.

5. The most disappointing feature of the plot was its failure to draw previously unrecorded species; but its failure to attract crows, starlings,and house sparrows that would have been unwelcome was some compensation.

6. Outstanding shortcoming of this and other feed patches is the short period of availability of seed. This one was practically exhausted by mid-November.

7. An abundance of readily available feed in fall did not appear to alter the dates of occurrence of migrants. However, a few summer resident species that formerly left the Sanctuary in July and August lingered into October and November after the feed patch was established.

8. An annotated list of the species making more than incidental use of the feed patch is given, with observations on the usefulness of the plot to them and its influence on their behavior.

9. Aside from the insectivorous northern yellow-throats, and the sunflower-loving blue jays and chickadees, all of the regular occupants of the patch were seed-eating fringillids.

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THE YIELD AND PERSISTENCE OF WILDLIFE FOOD PLANTS

Barry C. Park

This four-year study was carried on during the years 1935 to 1938, inclusive, on the Monongahela National Forest in West Virginia. Most of the field work was done by S. S. Dietz, former Wildlife Technician on the Forest, and the compilation of the data was by W. E. Roberts, Timber Management Staff Assistant. The purpose of this investigation was to determine the annual bearing volume, ripening and maximum persistence dates of fruits for forest wildlife food-bearing shrubs and trees.

Field Method and Compilation

The data on volume of yield, percentage of plants bearing, and the persistence of the fruit were obtained for a total of 27 species.

Averages given for the period of the study for each plant are arithmetical because this average gave the truest figure for the "yearly average."

Each plant observed was permanently marked and the same species of plants were observed annually at various locations on game range survey lines scattered over one and one-half million acres of forest. The annual yield and persistence for each species were determined by arithmetical averages.

Ripening

The ripening date for all species was found to be very consistent. It did not vary more than a few days for most of the species studied, 15 days being the maximum variation for any one species. Table 1 gives the average ripening dates for all species observed.

Persistence of Fruit

The annual variation in persistence was considerably less than the variation in yield.

For most species the variation in persistence was only a few days, but one species, seedling apple (*Malus pumila*), varied as much as two months. It appears that this fact should be given consideration when collecting apple seeds for wildlife food planting projects. The usual practice has been to select seed from trees which hold their fruit the longest. From the findings of this study it seems that it would be better to observe those trees having the most persistent fruit for several years to determine which trees were the most consistent in their ability to hold their fruit late, and then gather seed from those trees.

Yield

The average figures on yield for the majority of the species observed mean little because the variation from the average for a single species was so great. (See Table 1.) For example, the two heaviest producers, American beech (*Fagus grandifolia*) and Hawthorn (*Crataegus sp.*), varied 95+ and 67+ quarts, respectively. The maximum variation in yield figure given in Table 1 was obtained by subtracting the lowest from

TABLE 1

YIELD AND PERSISTENCE OF WILDLIFE FOOD PLANTS MONONGAHELA NATIONAL FOREST, W. VA.

Scientific Name	Common Name	Average		4 Years Crop Average					Years crop failed	Max. for 4-Yr. Period	
		No. Studied yr'ly	Diam. stem in inches	% Plants bearing	No. qts. produced	Date of ripening	Max. date persistence fruit on plant	Ave. date ripening		No. days variation in persistence	No. qts. variation in yield
Amelanchier canadensis	Downy serviceberry	20	3.23	78	2.42	7/3	8/1	7/3	1938	None	4.36
Cornus alternifolia	Pagoda dogwood	18	1.00	44	.09	8/20	11/15	8/20	1936, 1938	10	.22
Cornus florida	Flowering dogwood	8	2.00	71	.50	9/20	12/2	9/20	1936	25	1.21
Crataegus	Hawthorn	9	2.73	69	37.00	9/20	10/31	9/20	1938	10	95.88
Fagus grandifolia	American beech	34	11.40	41	20.7[1]	9/25	10/31	9/25	1936, 1938	3	67.3
Ilex decidua	Winterberry	10	.90	75	.83	9/22	spring	9/22	No failure	None	.07
Ilex montana	Mountain holly	7	1.60	53	.27	9/20	1/5	9/20	1936, 1938	10	.16
Malus pumila	Apple	24	4.10	44	2.46	9/10	11/21	9/10	1936	59	5.62
Prunus americana	American plum	5	2.80	67	1.80	9/12	10/8	9/12	1936	15	2.60
Prunus serotina	Black cherry	9	8.30	43	1.98	9/7	10/17	9/7	1937	5	5.60
Prunus pennsylvanica	Pin cherry	10	4.70	50	.68	8/31	10/6	8/31	1937	25	1.32
Malus coronaria	Wild sweet crab	15	1.78	52	.22	10/9	11/2	10/9	No failure	6	.28
Quercus alba	White oak	23	7.20	28	1.00	10/3	11/29	10/3	1936, 1937	6	2.00
Quercus borealis	Red oak	10	6.60	45	.45	10/12	11/28	10/12	1937	6	.45
Quercus marilandica	Black jack oak	10	.87	24	.012	10/2	12/15	10/2	1937, 1938	30	.005
Quercus prinus	Chestnut oak	14	7.50	33	1.30	10/13	11/20	10/13	1936, 1937	20	2.5
Quercus rubra	Southern red oak	12	6.80	21	.555	10/12	11/20	10/12	1937	20	1.494
Quercus velutina	Black oak	3	5.30	33	.43	10/3	11/15	10/3	1937	10	.44
Rhus typhina	Staghorn sumac	28	1.50	47	.15	9/1	spring	9/1	No failure	none	.09
Rubus allegheniensis	Allegheny blackberry	40	.29	60	.037	8/7	9/31	8/7	No failure	20	.058
Sambucus canadensis	American elder	9	.40	81	.41	9/12	10/5	9/12	No failure	10	.77
Sambucus pubens	Red-berried elder	10	.47	70	.081	7/9	8/10	7/9	No failure	20	.098
Smilax	Greenbrier	22	.25	39	.040	10/15	spring	10/15	No failure '36, '38 very light crop	none	.116
Viburnum acerifolium	Maple leaf viburnum	12	.33	60	.011	10/27	12/8	10/27	No failure	15	11.0
Viburnum alnifolium	Hobblebush	29	.55	40	.034	9/22	11/10	9/22	1938	15	.073
Vitis cordifolia	Frost grape	11	.90	63	.73	10/7	spring	10/7	No failure	none	1.03
Vitis vulpina	Riverbank grape	7	.86	36	.172	10/2	11/10	10/2	1937	15	.497

[1] Unshelled nuts—to obtain volume of nuts, divide by 3/8.

the highest yield for each species during the four years; failure years were not considered. The maximum variation figure was generally considerably higher than the average yield figure for the four years.

The information of importance to the wildlife manager concerning yield is the variation in crops from year to year. An environmental improvement program should include a variety of species. It might even be wise to include a few of the less palatable species, such as Staghorn sumac (*Rhus typhina*), which has fruit persisting until spring and is a very stable producer. The choice should include Winterberry (*Ilex decidua*), Greenbrier (*Smilax*), and Frost grape (*Vitis cordifolia*), since they are consistent bearers, with fruit persisting until spring. Other good and consistent bearers are Wild sweet crab (*Malus coronaria*) and Mapleleaf viburnum (*Viburnum acerifolium*), along with such species as Flowering dogwood (*Cornus florida*), White oak (*Quercus alba*), Chestnut oak (*Quercus prinus*), American beech (*Fagus grandifolia*), and Apple (*Malus pumila*).

PERCENTAGE OF PLANTS BEARING

The average percentage of plants bearing fruit was found to be 70 per cent or higher for the following species: *Amelanchier canadensis, Ilex decidua, Sambucus canadensis,* and *Sambucus pubens.*

The oaks as a group were lowest, with Southern red oak (*Quercus rubra*) poorest, with only 21 per cent. Fortunately, the most consistent bearers, with fruit persisting until late winter or spring, have a good percentage of plants that bear fruit. (See Table 1).

SUMMARY

1. This study covers four years' observation on 27 species of wildlife food-bearing shrubs and trees on the Monongahela National Forest, West Virginia.

2. Each plant was permanently marked and the same plants were observed annually at various locations on game range survey lines scattered over one and one-half million acres of forest.

3. Of the species observed, all bore fruit in 1935; 33 per cent failed to bear in 1936; 33 per cent again in 1937; and 29 per cent in 1938.

4. Six species or 22 per cent failed twice in the four-year period.

5. Nine species or 33 per cent produced a crop every year.

6. The most consistent bearers, with fruit persisting until late winter or spring were: *Ilex decidua, Rhus typhina, Malus angustifolia, Smilax, Vitis cordifolia,* and *Viburnum acerifolium.*

7. The most prolific producers were: *Amelanchier canadensis, Crataegus, Fagus grandifolia, Malus, Prunus americana,* and *Prunus serotina.*

White and chestnut oaks were very good producers but only about a third of the trees yielded acorns.

8. The variation in persistence of fruit for most species was only a few days.

9. Seedling apple trees varied considerably in their ability to hold fruit; variation was greater than for any other species, 59 days.

10. Average figures on yield mean little, because variations from the average were so great. American beech (*Fagus grandifolia*) and Hawthorn (*Crataegus*) varied 95 and 67 quarts, respectively, from the arithmetical average

for the four years, failure years not included.

11. The maximum yield variation figure was generally much higher than the average yield figure for the four years.

12. The most consistent bearers, with fruit persisting until late winter or spring, generally have a good percentage of plants that bear fruit.

13. The most important factor concerning yield, so far as the Wildlife Manager is concerned, is the variation in the total annual yield of wildlife food on a given area.

CONCLUSION

From a practicable management standpoint, the variety of species of wildlife food plants rather than the number of specimens of one or several individual species is the factor that makes a good environment for wildlife insofar as the yearlong food, and especially the winter food supply, is concerned. With variety, the possibilities for wide fluctuations from year to year in the winter-carrying-capacity of a good environment are not great. The annual variation in yield and persistence of wildlife food plants can probably never be effectually controlled in the management of large areas of wild land and, therefore, the plan of management that provides for the greatest variety of species of wildlife-food-producing plants will assure the most stable environment.

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DEFENSIVE CONTROL OF RODENTS AND RABBITS

Philip F. Allan

Rodents present some of the most challenging problems to wildlife management. Although policies as to their control have been the subject of controversy, most biologists will agree that there are circumstances under which large populations of rodents are inimical to man's interests (See Taylor (34)). The methods of control, rather than the needs, however, are most frequently challenged. A multiplicity of factors enters into each problem. Some of these are: land values, land product values, nature and amount of damage, costs of control, results of control, and effects of control on the remainder of the biota. Drastic, and sometimes ludicrous, measures, such as that reported by Woodruffe-Peacock (42), are frequent in rodent control; often with a similar climax. He states that starlings in England roosted on blackthorns in such numbers as to break down many branches. The usurpation of woodpecker holes caused more holes to be dug, promoting the entrance of fungus growth. The blackthorns were finally cut down to save them from complete destruction! It is altogether too easy, ecologically speaking, to cut off the nose to spite the face. Taylor (35) gives a basis for biological approach to rodent problems in his paper, *Some Effects of Animals on Plants*, that is well worth the attention of wildlife managers (See Van Dersal (36) and Bond and Borell (5) also).

A review of examples of defensive control of rodents may be pertinent in pointing the way for further discussions and practice both in the field of research and in practical application. So far as possible, these examples have been classified into related groups and are discussed in relation to their proved merit. The purpose of this paper is to summarize the literature on defensive control and to present observations of the writer and others bearing upon that type of control. Some of the examples, although not the result of experimentation or specific studies, are considered reliable. The writer does not advocate the adoption of the practices reported without further investigation of their merit. Each instance of damage by rodents presents its own problems, which should be approached in a sound technical manner.

From an ecological viewpoint, the control of animal populations on a permanent basis must depend upon a change of the environment either in favor or disfavor of the animal species. Control of populations without environmental manipulation, short of the annihilation or continued artificial propagation of the species, must fail or, at best, be only semipermanent in results.

Wildlife management is largely a naturalistic approach to the control of the animal populations through manipulation of environment. If wildlife managers are capable of increasing desirable animal populations, principally through ecological operations, they should by the same token and using similar tools, be able to decrease undesirable populations. The entomologists, and particularly the malariologists, have long used

ecological methods for the control of insect pests, and we can well turn to them for the definition of the type of control necessary to deplete undesirable animal populations. Paraphrasing the definition of Hackett, Russell, Scharff, and White (16): Defensive methods may be defined as the deliberate extension or intensification of natural processes that tend to limit the production of animals or their contact with man. Under the conception of these writers this implies that direct toxic and mechanical measures of *destruction* are "... properly distinguished from measures designed to bring about a change in natural conditions of a permanent or semi-permanent kind so as to create a new and relatively stable situation unfavorable to the life and activity (of the species[1])." These authors present an outline of naturalistic control for mosquitoes which has been followed, essentially, in this paper summarizing available information with respect to rodents and rabbits.

With few exceptions, defensive means of controlling rodents have been of suggestive value only. A search through a considerable amount of literature reveals only seven such practices of proved value. These are: tillage practices, destruction of cover, flooding, fencing, changing environment by burning, or by grazing, and the use of "buffers." In one additional instance, biological knowledge enabled preventive measures to be taken prior to an increase in microtines, while in two others, providential circumstances reduced rodent populations. As will be pointed out below, a few measures of definite value have been used, the records of which do not, to the writer's knowledge, appear in publication. It seems especially regrettable that not one reference was found in THE JOURNAL OF WILDLIFE MANAGEMENT.

[1] Insert mine.

PHYSICAL CONTROL MEASURES

Destruction of Habitat.—Clean tillage of orchards, recommended in many publications, can be considered of proved efficacy in the control of small rodents. It has long been a practice of orchardists the country over. Silver (29), Spencer (32), Whitehead (40), and others have advocated this type of control, but it certainly merits further investigation, especially since the use of cover crops is recommended widely for soil conservation in orchards. R. M. Bond, in a letter, states that "severe (to two inches) grazing of permanent cover crops in orchards" is advocated by the Soil Conservation Service in the West Coast Region for mouse control. The mice are thus exposed to predators. The grazing is done with sheep after fall harvest and does not injure the cover to the extent of permitting soil erosion. The destruction of vegetational cover, however, should always receive careful consideration from the viewpoint of its effects on other animal life. Clearing of hedgerows has been advocated for rodent control. Such clearing is likely to be detrimental to game or other wildlife and its effectiveness seems to be questionable.

Hamilton (17) records an interesting application of biological knowledge when a forecast of a high point in the cycle of microtines enabled orchardists in New York State to prevent damage through clean tillage and other practices.

Bond (ibid.) points out that where annual ditches are used in sandy soil inhabited by kangaroo rats, scarifying with straight-set discs is of value in breaking up burrows and driving out the rodents without much disturbance of plant growth or mulch. Hawbecker's (18) studies on *Dipodomys venustus* further confirm the value of this method of control. Subsoil cultivation might accomplish the same result with pocket gophers. In an investigation to determine whether kangaroo rats were damaging earthen structures as terraces and diversions, the writer found that the animals were less populous and damage was less apparent in cultivated than in fallowed structures. In the instance studied, in northeastern New Mexico, the hazard from rodents had been greatly over-rated.

Trampling of earthen fills by livestock is sometimes recommended as a preventive of rodent damage. This suggests other, and probably, more effective means of compacting such works during, or shortly after, construction. Where applicable, packing should keep out weakly fossorial rodents such as the kangaroo rat. However, no specific instance of packing structures for rodent control has come to the writer's attention.

The use of fire as a means of habitat destruction may be suggested as a field for study. In some instances, to the writer's knowledge, it is used by ranchers in the Texas Panhandle to control wood rats. Here, however, control may be unnecessary and undesirable, since the rats may be of little economic significance or even beneficial. The effects of burning of vegetation on soil erosion should be kept in mind in connection with any control by fire. Baker (4) and Vestal (37) point out that burning, grazing, and clearing generally reduce rodent populations, particularly those of wood rats. Clements (7), Greeley (15), and Hofmann (21) report evidence supporting a similar effect of fire in forests. It is presumed that the results cited by these authors are incidental to operations that were not specifically done for the control of rodents. It should be noted that the use of fire for habitat destruction is here differentiated from burning to bring about changes in plant succession.

Beaver and muskrat damage is sometimes severe in irrigated areas. In the case of the beaver, at least, the destruction of habitat might be easily accomplished by removal of trees, yet a cover of grasses or legumes could be maintained for ditch stabilization. The destruction of muskrat habitat might be brought about by the reverse process; i.e., replacement of low plant growth by trees.

The possibilities of shading out undesirable rodent populations probably has not been much explored. Shading is successfully used in the control of certain insects, and may offer a field for investigation in connection with control of some species of rodents.

Flooding is considered valuable in the control of pocket gophers by Crouch (8), although, of course, it is not susceptible of general application. Chapman (6) records a considerable destruction of Norway rats by providential flooding. Proper use of irrigation in orchards may also be a means of controlling orchard-dwelling rodents. The Page ranch in Arizona, a discussion of which has been published by Musgrave

(27), demonstrates not only the control of rodents by flooding but also of practical ecology in utilizing their burrows to improve plant growth. Musgrave quotes Page as follows: "Every time we had a rain I took my shovel and dug ditches to run as much water as I could into the rats' and ants' nests. . . . After a while I noticed that the bare spots around them were covered with thick feather grass. . . . What had been eye-sores were now the best places on the half-section." This article is well worth the attention of plant and animal ecologists.

Creation of Non-living Barriers.—Fencing is probably the most commonly used means of preventing damage from rabbits, mice, rats, gophers, and other rodents. There are a great many references on the subject, and it is a generally accepted practice. Fencing may include a whole plantation or an individual plant, but the principle is the same. Likewise, the wrapping of trees with paper, cloth, and yucca leaves is a form of fencing. All have been used successfully. Fencing, generally, is more economical than continued replanting and is fully as satisfactory as poisoning. Various containers are employed to protect the roots of seedlings from pine mice. Dixon (9) has suggested the use of a cement core in the center of canal banks to prevent damage by pocket gophers. Allan and Davis (1) have recommended a layer of sand to prevent muskrats from burrowing in earthen dams. This method was used successfully in one instance by the Soil Conservation Service in preventing crayfish damage. Asphalt, concrete, sheet metal, wood piling, or wire might be used in earthen structures to prevent rodent damage. Undoubtedly, all of these have been tried, but the writer has no knowledge of the success of their use. Telephone and other companies that use insulated wires underground often encounter difficulty from pocket gophers. They find it necessary to protect wires and cables by a steel casing in areas where pocket gopher populations are large.

The rodent-proofing of buildings is too well known and generally applied to warrant more than passing notice here. See. U. S. Dept. Agr. Farmers' Bulletin No. 1638, *Rat Proofing Buildings and Premises* (30).

BIOLOGICAL CONTROL MEASURES

Natural Enemies and Diseases.—Much of the literature on predator-rodent relationships points out the chiefly beneficial food habits of most predators, and a few show the harmful effects of predator control in increasing rodent populations. The Wisconsin Conservation Bulletin (2), for example, reports "over-trapping of predators has brought a mouse plague to some sections of Wisconsin the past winter." Dymond (10), Errington (11), Errington and Breckenridge (12), Snyder and Hope (31), and many others, have discussed predation on rodents, pointing primarily to the relation of availability of prey to the degree of predation. An instance is known to the writer in which a Pennsylvania orchardist was able to attract many screech owls to his land by furnishing bird boxes. During one year he had 13 or 14 pairs using the boxes, and was satisfied that they had an appreciable effect on the mouse population. Sparrow hawks, barn owls, and barred owls might be attracted in the same

way. He also captured black snakes and other non-poisonous species and released them in the orchard, although the success of this measure is unknown. Skunks also were protected by this orchardist and various shelters such as tiles were provided for them.

Frequently, farmers protect bull snakes in their fields and sometimes release them in barns and granaries. However, such practices must be of little permanent value unless steps are taken to increase the snake population over what normally occurs on farm land.

Bond (ibid.) states that the Soil Conservation Service advocates the erection of poles with cross perches in treeless alfalfa fields to attract barn owls for the control of meadow mice; while Leopold (in conversation) suggested small plantings of cottonwoods, well scattered in the Plains area, to attract nesting hawks and great horned owls. E. Lowell Sumner, Jr., in a letter, tells of a relationship of eucalyptus growth to barn owl populations of considerable value. Hedgerows of tall, dense-topped trees were found to harbor large numbers of owls, and to provide nesting and roosting sites for red-tailed hawks, sparrow hawks, and screech owls, as well. In a 4-acre woodlot, Sumner noted a relatively stable population of 50 barn owls that persisted until the woodlot was cut down.

The writer here suggests, for study purposes at least, the possibility of attracting burrowing owls to sites populated by kangaroo rats. A posthole digger might serve to start a colony. Cannot weasels, skunks, badgers, raccoons, swift foxes, and other predators of rodents be similarly encouraged?

From a practical standpoint efforts to increase the animals predatory on rodents probably should be accompanied by measures to expose the prey to them.

The importance of diseases is emphasized in various publications on rodent control. Yet surprisingly little actual use of this means of control is on record. Commercial concerns, from time to time, bring out viruses and diseases claimed to control rodents. It is probable that all of these have been failures. Yet Hamilton (17) and Crouch (8) hint at the possibility of control by these means, although the latter questions the likelihood of success.

Changing Flora and Fauna.—Despite the general acknowledgment among biologists that rodents in pest proportions are a successional phenomenon, very little work has been undertaken to combat rodent populations through ecological corrective measures. Man, as a superdominant, sets the stage for secondary successions in both plants and animals; but more often than not, does little to remedy the hardships thus imposed upon himself through adoption of measures designed to return the climax. He rather prefers stop-gap means of no lasting value. Hinton (20) sums up the need for an ecologic viewpoint of mammal problems when he states, "Finally, man must, in order to feed himself, interfere with the face of the earth. But he should be alive to the possible consequences of that interference. In every community, actions of these kinds should be guided by biological experience and opinions. Watchfulness upon the great openings which we create for animals is what is chiefly needed; we should be quick to prevent

if we wish to control." The most notorious achievement of man in opening the way for rodents has occurred, undoubtedly, in the case of house mice, black rats, and Norway rats. Komarek (22) suggests that something similar has occurred in relation to some of our native rodents.

Outstanding success in the control of rodents by changing the flora has been achieved by Stoddard, and other workers, in the Southeast. Using fire, Stoddard (33), says, "we control the cotton rats and the troubles that come with them, largely through control of their surroundings, rather than by direct action against the rats themselves." Komarek (23) further states, "As a practical management measure we find that it is only necessary to keep the land from becoming optimum cotton rat habitat, largely by the use of fire." He also points out other changes in rodent species through plant succession. Flint (13) records considerable damage by rodents in forest replantings following fire, where it may be assumed that the plant succession provided a suitable habitat for the animals. This report from Montana contrasts with the findings of Clements (7) in Colorado.

The "animal weed" theory has received wide recognition. Leopold (25) points out the possibility of "biotic farming" with regard to rodents. This means a conscious effort to carry the biota to levels more satisfactory to man.

The control of grazing as a means of bringing about ecological changes in rodent population on the range deserves much greater consideration than it has ever received. In the West, where range land predominates, the demands for rodent control are most vigorous. These demands seem to be corollary to overgrazing by livestock. It is surprising that so little "biotic farming" has been done on range lands when the possibilities are so great and the need so urgent.

Vorhies and Taylor (39) suggest ecological control, where necessary, of white-throated wood rats (*Neotoma a. albigula*), through the maintenance of climax grasses, since these rodents are an accompaniment of the brush and weed stages of plant succession. Experiments on the relation of plant succession to pocket gopher populations reported by Garlough (14) indicate that control of grazing by livestock brings about reduction of this rodent. In their study of jack rabbits, Vorhies and Taylor (38) state, regarding the scarcity of jack rabbits in the better-grassed areas, "This observation has a very practical bearing. It indicates that the stockman will make no mistake in conservative handling of his range; that jack rabbits will not necessarily increase to consume the surplus of grass left by cattle; and that if a range is allowed to run down, jack rabbits are likely to become more, rather than less, abundant, at least up to a certain point."

Cannot cropping systems be so designed as to discourage the presence of rodents? Bond (ibid.) advocates arranging or changing crop rotations in areas infested with meadow mice so that the row crops (with scanty ground cover) come in years of high points in the cyclic fluctuations. Lantz (24), speaking of thickly-sown cane or kafir corn, states, "With good rains this will grow faster than the animals (i.e., prairie dogs[2]) can cut it down."

Komarek (22) records complete local

[2] Insert mine.

faunal changes produced by manipulation of habitat. The section of the present paper on "Natural enemies and diseases" indicates further possibilities in this direction.

Factors inherent within every species limit populations even in optimum habitats. Biologists, apparently, have consistently overlooked the possibility of using those factors for control. Perhaps they are unusable; yet the very animals themselves may hold the key to control. Hinton (l.c.) reports a fantastic scheme devised by Mr. Rodier, of Australia, for the extermination of rabbits. This was the only reference found hinting at species control. The system, based on unbalancing the sex ratio (by trapping and destroying females) has been thoroughly discredited by Hinton.

Creation of Living Barriers.—The creation of living barriers differs from the following section, "Diversion to other habitats," in that the barrier results from a change, making a habitat impenetrable, while diversion may involve making a new habitat without changing the old, or, to use a popular term, creating a "buffer."

No reference was found that could properly be classified under this section. Yet, certain possibilities suggest themselves. Densely fibrous-rooted plants, or plants that form a tough sod, might conceivably prevent weak burrowers from invading the soil. Are certain species of plants repellent to rodents? A persistent rumor, probably exploded, places castor bean plants in the role of a barrier to moles. Despite the general fallacy of such rumors, certain plants may actually have these qualities. Drawing, again, on the experience of the entomologists, we find that Hawley and Metzger (19) state that certain food plants eaten by the Japanese beetle are toxic, notably—geranium, certain strains of castor beans, silverbell (*Halesia tetraptera*), and the bottlebrush buckeye (*Aesculus parviflora*). It should be noted that the authors do not commit themselves as to the use of these plants for the control of the Japanese beetle.

Diversion to Other Habitats.—Here, again, there is little evidence that control has actually been accomplished by diversion. Perhaps the only work classifiable in this section is that of creating conditions attractive to rabbits adjacent to, but outside of, orchards and other tree plantations. Siegler (28) quotes from an unsigned paragraph in the Pennsylvania Game News of August 1934, "J. W. Hershey, a Nurseryman of Downington, and others have found by extensive experience that planting soy beans near your trees and leaving a patch of them to stand over winter, will keep rabbits from gnawing shrubs and trees." This type of practice has been tried elsewhere with varying degrees of success. Siegler goes on to discuss other "buffers" against rabbit damage, among them, brush piles of palatable food plants.

Trap crops are commonly used in the control of insects (see, for example, Marcovitch (26)). Their use in rodent control may offer possibilities. William R. Van Dersal (in a letter) points out the practice of California farmers in putting a hay crop around the edges of fields adjacent to brush. The idea is that the succulent green material is more attractive to the rabbits than the more valuable crops within the fields.

There is, of course, considerable likelihood that even though more attractive habitats are provided, the population of infested areas will not be materi-

ally changed, but in combination with other naturalistic measures there may be merit in this type of treatment.

Control in the Creation of New Environments.—Man seems to have a peculiar genius for creating environments particularly adapted to the welfare of rodents. Hinton (l.c.) states that, "If you create a vacancy, it is your own very difficult business to keep it vacant" (See also Vorhies and Taylor (38), p. 576).

What can be more ideal for a kangaroo rat than a newly constructed terrace? The loose earth is easily penetrated, and shortly there will be a crop of annual weeds to keep the larder of *Dipodomys* well stocked with seeds. One of the most admirable examples of the creation of a kangaroo rat habitat to come to the writer's attention is to be found in northeastern New Mexico. Here, on a field blown clear of top soil to the hard pan, and formerly impenetrable to the rats, a series of terraces was built. Construction was by means of furrows plowed on the contour. In them were placed Russian thistles, and soon dust storms built up a fine system of terraces. It was a novel idea and worthy of further study, but the terraces were "made to order" for kangaroo rats. A good rain, shortly thereafter, resulted in a dense stand of wild sunflowers. Within a year, the terraces were literally honeycombed with the burrows of kangaroo rats (*Dipodomys ordii*).

Bond (ibid.) suggests a simple means of terrace construction to prevent kangaroo rat damage: "Avoid the use of narrow-base terraces (a former favorite device), especially in sandy soils. Where they are used they are so designed that normal flows are confined to the ditch section, the fill section serving merely as a safety factor." Aylen (3), in a statement of the advantages of the broad ridge (i.e., terrace) in South Africa, lists: "The damage done by rats and the natives hunting for them is very considerably reduced." The Soil Conservation Service engineers consider the broad-base terrace, used in the Southern Plains, less susceptible to rodent damage than structures of other designs.

It is often feasible to substitute species of plants low in value, for those attractive to rodents. On an area well populated with fox-squirrels that was being planted to trees, the writer made the obvious suggestion of substituting elm for walnut which, after two years of seed spotting, had provided fat squirrels but no trees. Catalpa and Asiatic elm are seriously harmed by rabbits, but osage orange is not. The last is a logical substitute, therefore, unless the need for catalpa and elm is preponderant.

In areas of high rodent hazards, should not the biologist suggest crops immune to damage if they serve equally as well as those susceptible?

CHEMICAL CONTROL MEASURES

Creation of Chemical Barriers, Use of Repellents.—The use of chemical repellents for prevention of damage to trees by rabbits and mice has been vastly explored, but the only successful repellent to come to the writer's attention is correctly prepared sulfonated oil, which seems to prove effective against cottontail rabbits. Many chemicals have been tried, the odor, taste, color, or contact with which are supposed to repel rodents. Various oils and oil derivatives are the basis of many of the so-called repellents. Tar is recommended by Whitehead (41) as a treatment for corn

repellent to kangaroo rats. Red lead, nicotine sulphate, and a wide variety of other chemicals tried by A. C. McIntyre (conversation) at Pennsylvania State College, did not prevent chipmunks and gray squirrels from eating treated nuts.

Among the interesting theories on repellents are two worthy of mention. On the assumption that droppings, especially those of a different species, are repellent to animals, Don G. Fawcett, a Soil Conservation Service technician, suggested the use of the pellets of domestic hares mixed with an adhesive as paint for trees to protect them from jack rabbits. Van Dersal (letter) proposes a repellent composed of weasel musk on the theory that rodents fear weasels and will avoid places apparently frequented by them. Experiments on repellents thus might include tests as to whether odors from the principal enemies of the rodent species would prove a deterrent.

The possibility of using chemical repellents in earthen structures has been considered by the writer. The Bureau of Chemical Warfare was requested to suggest caustics that might be used for this purpose. However, no information was obtained, except that mustard gas, even in very dilute form, is too dangerous to use. It is possible that a viscous oil might repel kangaroo rats.

CONCLUSION

It may be pointed out that there are several aspects of rodent control, apart from methods, that should receive consideration. Since the whole problem hinges on economics, either directly or indirectly, it is the duty of the wildlife manager to include this factor in his approach to rodent problems. It is not infrequent that the cost of control far exceeds the values realized either to the land or to the crops protected. Defensive methods should be so designed that they are economically practical and of permanent value. In the permanence of non-aggressive control may rest the most important reason for its use.

Finally, the writer wishes again to emphasize that we do *not* now know how to control rodents by use of natural defenses, nor are most of our research enterprises designed to enlighten us. This is a field of wildlife management that has been largely neglected. The progress of rodent control research has been chiefly along the line of getting better artificial control. Particularly in studies for the improvement of range management, the rodent factor has been overlooked or dismissed with recommendations for artificial control. During recent years, many millions of dollars have been spent in efforts to discover methods of increasing desirable forms of wildlife, but only a few hundreds are being devoted to studies that may yield information of value in decreasing undesirable wildlife populations in a sound ecological manner.

SUMMARY

1) Defensive methods for the control of rodents are those designed to bring about a change of natural conditions of a permanent or semipermanent kind unfavorable to the species.

2) Such changes may be physical, biological, or chemical.

3) A few defensive measures are of some proved value—namely, tillage practices; grazing of cover crops; destruction of cover by fire; flooding; fencing; encouragement of natural enemies; changing flora by use of fire;

changing flora by use of grazing; diversion to habitats immune from injury; and chemical repellents.

4) Most defensive measures have been of suggestive value only.

5) More research and trials are needed.

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COTTONTAIL RABBIT NESTS AND NESTLINGS[1]

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During the spring and summer of 1939 a study of the nesting activities of the cottontail (*Sylvilagus floridanus mearnsi*) was made in Pennsylvania, and the results were published by Beule (1940). The study of this important phase of the life history of the cottontail was continued in the typical farming country of Centre and Lycoming Counties, Pennsylvania, during the breeding and nesting season of 1940. This paper presents the results of that investigation and a comparison of the data for the 2 years.

The work was done under the supervision of Dr. Logan J. Bennett, Biologist, U. S. Fish and Wildlife Service; Dr. P. F. English, Associate Professor of Wildlife Management, Department of Zoology and Entomology, The Pennsylvania State College; and Richard Gerstell, Chief, Division of Propagation and Research, Pennsylvania Game Commission. The writers are also especially indebted to Roger M. Latham, Game Research Assistant, Pennsylvania Game Commission, for valuable aid during the 1940 study.

The Nesting Period

In Pennsylvania the usual cottontail nesting period extends from the middle of March through September. Nesting activities before March 15 and after September 30 apparently involve only a small part of the cottontail population and are of minor importance. During the two breeding seasons studied, May appeared to be the most effective nesting month, although April, June, and July were also of considerable importance.

Hamilton (1940) stated that mating in New York State was apparently delayed in 1939, and the writers' field work in Pennsylvania led to a similar conclusion (Table 1). The field work of 1939, however, was not started until April 1.

Table 1 presents the approximate birth dates obtained by three methods for 204 cottontail litters. Birth dates were estimated from the sizes of the nestlings, from the sizes of embryos removed from pregnant does, and from the condition of successful old nests. Although the information thus obtained is approximate, it appears significant when tabulated by months.

Location of Nests

Because cottontail nests were found in a number of cover types, an attempt was made to evaluate these types as

[1] Paper No. 26 from the Pennsylvania Cooperative Wildlife Research Unit, the Fish and Wildlife Service (U. S. Department of the Interior), the Pennsylvania State College, the Pennsylvania Game Commission, and the American Wildlife Institute cooperating.

Authorized for publication on April 15, 1941 as Paper No. 1029 in the journal series of the Pennsylvania Agricultural Experiment Station.

[2] Co-leader, Pitman-Robertson Project Penna. No. 6-R, "General Ecological Investigation." A portion of this paper represents a report on one phase of the Federal-Aid Project, conducted in conjunction with a long-term investigation previously undertaken by the Cooperative Unit.

TABLE 1

BIRTH MONTH OF 204 COTTONTAIL LITTERS

Month	1939		1940	
	No. of litters	Percent of total	No. of litters	Percent of total
March	0	0.0	3	2.7
April	2	2.2	32	28.3
May	44	48.4	39	34.5
June	22	24.2	21	18.6
July	17	18.6	10	8.8
August	2	2.2	5	4.4
September	4	4.4	3	2.7
Totals	91	100.0	113	100.0

nesting areas. The approximate acreage of each cover type searched for nests was recorded, and from these data the approximate number of acres to a nest was obtained. This method of evaluation indicated that although more nests were found in fallow fields than in any other cover type, fallow fields did not have the greatest density of nests. Unkept orchards held 1 nest to 1.54 acres, whereas fallow fields contained 1 nest to about 13 acres. The data in Table 2 indicate that unkept orchards and young pine plantations are important nesting areas, although only 15.7 per cent of the total of 121 nests were located in these types.

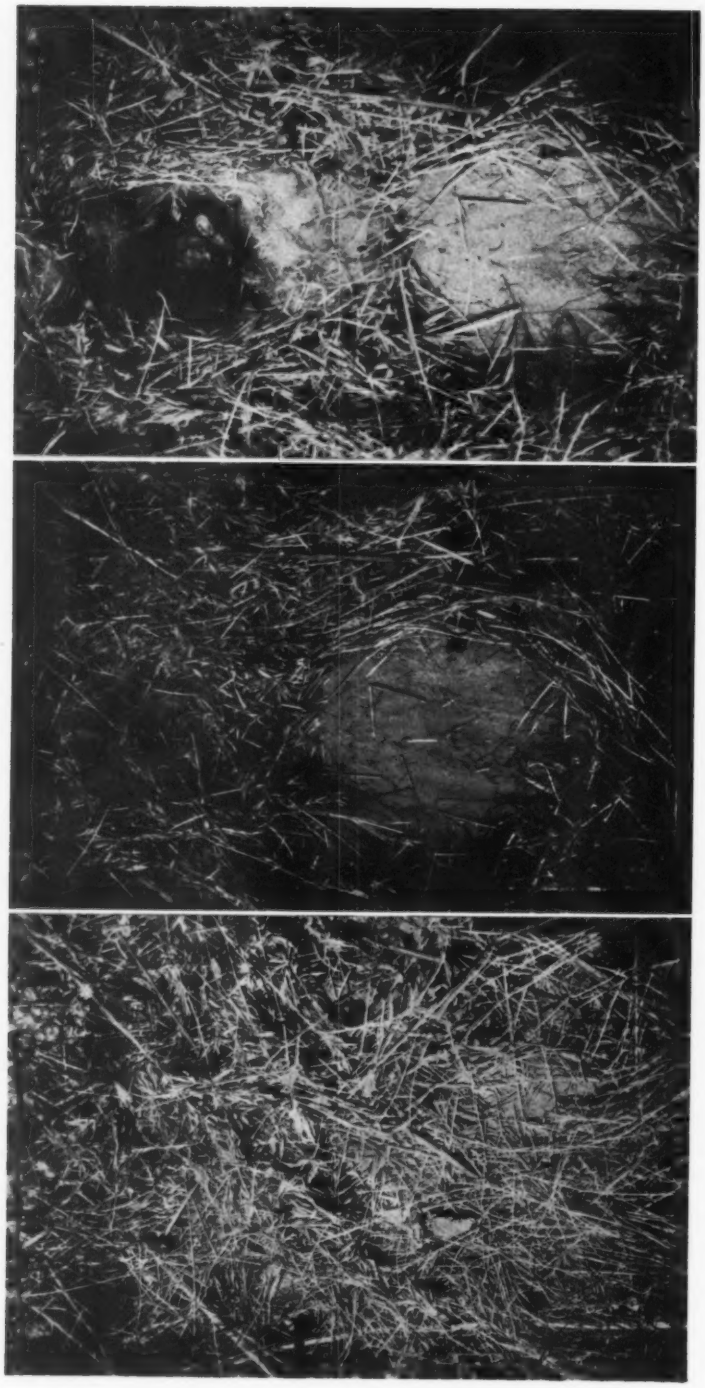
As herbaceous cover grew after nest destruction or abandonment, only cover around functional nests was evaluated. This evaluation was made by measuring the density and height of the vegetation on a mil-acre plot surrounding the nest. The data obtained on 23 nests in use showed a wide range in the height and density of cover. No nests were found in areas devoid of cover.

Some cottontails selected peculiar locations for their nests. One nest was found in a rockpile at the edge of a field; a nest in a manure-pile was recorded by Beule (1940); and in the crotch of a willow tree, 9.5 feet above the ground, a nest containing five young was ob-

TABLE 2

NESTING SITES AND SUCCESS OF 121 COTTONTAIL NESTS

Cover type	No. of nests	Successful	Unsuccessful	Undetermined	Percent successful	Approximate acres per nest
Fallow field	47	34	12	1	72.3	13.0
Hayfield	31	22	8	1	70.9	7.0
Unkept orchard	13	10	3	0	76.9	1.54
Young pine plantation	6	5	1	0	83.3	2.0
Pasture	5	4	0	1	80.0	14.0
Fencerow	7	4	3	0	57.1	10.9
Roadside	4	2	1	1	50.0	8.59
Woods	2	1	0	1	50.0	13.5
Lawn	2	0	2	0	0.0	Insufficient data
Beside structures	2	2	0	0	100.0	Insufficient data
Rockpile	1	0	1	0	0.0	Insufficient data
Golf links	1	0	1	0	0.0	Insufficient data
Totals	121	84	32	5		



A (*left*).—Appearance of typical cottontail nest. B (*middle*).—Cover material removed from nest and excavated earth. C (*right*).—The exposed nest and platform.

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served by Shadle (1940). Certain sites in orchards, plantations, and woods, however, seemed to be favored. Most of the nests observed in these types were at or near a tree or stump and opened away from it.

No choice of exposure, in regard to compass points, was apparent. Nests were found on all degrees of slopes from 0 to 35 per cent. All but two of the nesting cavities faced downhill. These two nests, on 5- and 15-per cent slopes, faced directly uphill; and both were successful.

CONSTRUCTION OF NESTS

A general description and measurements of cottontail nests were included in a previous report (Beule, 1940). Plate 8 illustrates a typical nest and how well it was hidden. Because most of the recent data corroborated previous findings, only new material and supplementary information on debatable subjects are here discussed.

Throughout this investigation observations have indicated that the nesting cavities were dug by the female rabbits. In 1940 a cottontail was seen with its front feet in the bottom of a typical nesting cavity; the cottontail had apparently sensed the oncoming observer and ceased to dig. The freshness of the excavated earth strongly indicated that the cottontail was responsible for the construction of the cavity. Two other cottontails were chased from freshly constructed nesting cavities, and subsequently both cavities were lined with grasses.

Cavities were known to have been lined with grasses on the first and second days after their construction, thus it was indicated that both operations were occasionally completed at the same time. Three nesting cavities were dug at least 6 days before the birth of the young, and corresponding periods of 12 and 17 days were noted for two additional nests.

Obviously, nesting cavities were often abandoned, especially if the grass lining or the surrounding vegetation was disturbed. Mice and skunks may often have pulled out the grasses or otherwise disturbed the lining, causing the cottontail to select a new nesting site. Two occupied nests were found short distances from abandoned cavities.

LITTER COUNTS

During this study 35 litters of nestling cottontails were examined and 9 sets of embryos were obtained from rabbits that had been struck by automobiles. Table 3 shows that the size of the litters ranged from 2 to 7, which corresponds to the figures given by Hamilton (1940). Seton (1929) gave the size of litters as 4 to 6 or 7 and rarely 3 or 8, whereas Gerstell (1937) found a range of from 3 to 8.

TABLE 3

NUMBER AND SIZE OF LITTERS IN 1940

No. of litters	No. of young in litter
1	2
3	3
13	4
12	5
9	6
6	7

The average number of young in a litter during the 1940 nesting season was 4.95. In 1939 the average for 26 litters was 5.42 (Beule, 1940). Generally the litters were larger during the first

TABLE 4

LITTER COUNTS OBTAINED BY MONTHS FOR 1939 AND 1940

Month	1939		1940	
	Litters examined	Average in litter	Litters examined	Average in litter
April	2	6.0	9	5.0
May	8	6.1	13	5.3
June	8	5.8	8	5.87
July	4	4.5	8	4.25
August	2	3.5	3	4.0
September	2	4.5	3	3.66
Totals and averages	26	5.42	44	4.95

half of the nesting season and became smaller as the season progressed. The same trend was observed in the number of litters examined. Table 4 records the number of litters and their average size by months during the 2 years.

DESCRIPTION OF NEWLY BORN COTTONTAILS

On September 15, 1940, a litter of five cottontails was found scattered through a pen in which a wild-trapped female was being held for experimental purposes. The female was known to be pregnant, and the pen had been examined the previous day. The young, therefore, were less than 24 hours old. They had already lost the extremely pink color characteristic of a litter of very young animals found in the wild: they were probably 15 to 20 hours old. Two of them were dead of exposure, and the remaining three were cold and wet. The more important measurements and weights, recorded soon after these nestlings were found, are presented in Table 5.

Cottontails are pink at birth, but the backs and sides of these animals were already darkened. A sparse covering of light-colored guard hairs was evident over the entire body surface. These hairs had reached a maximum development of 2 millimeters on the back but were scarcely $\frac{1}{4}$ millimeter long on the appendages.

The ears and eyes were tightly sealed, lines showing where their openings would appear. A pin-point opening was discernible at the apertures of the sex

TABLE 5

WEIGHTS AND MEASUREMENTS OF NEWBORN COTTONTAILS

No.	Total length	Tail	Tarsus	Weight
	mm.	mm.	mm.	g.
1	104	10	20	23.3
2	107	12	20	28.5
3	104	10	21	31.5
4	106	9	20	33.0
5	108	10	20.5	31.4
Averages	105.8	10.2	20.3	29.54

organs, and the opening to the anus was slightly larger. On the abdomen were slight protuberances—similarly developed on both sexes—where the teats would be. The teeth were generally undeveloped. The incisors had barely penetrated the gums, and the molars could not be seen. All the toes had claws less than 1 millimeter in length.

AGE DETERMINATION AND DEVELOPMENT OF NESTLINGS

To determine the ages of nestling cottontails, weights and measurements of all available nestlings were taken daily. Cottontails weighed approximately 25 grams at birth and averaged about 112 grams when they left the nest. Weight, however, was an unreliable indicator of nestling age, as a wide variation often existed among members of the same lit-

ter. Some litters also contained runts or exceptionally large individuals; and although this difference was sometimes apparent in the measurements, a wide variation always occurred in the comparative weights.

Daily measurements—including total length, tail, tarsus, and ear—were recorded for each nestling, and daily litter averages were then computed from these figures. Tail and total-length measurements were difficult to obtain on live animals and were discarded as practical indicators of age because of the probable errors. The ears of very young cottontails lacked the development necessary for exact measurement. Tarsal length proved a satisfactory index of age. This measurement was easily and quickly made, and showed little variance among individuals of the same litter. Although all available nestlings were measured, because of nest destruction, a complete series of measurements was obtained on only 19 litters. The daily tarsal-growth rate of all litters, without exception, was approximately 2 millimeters.

A working scale to determine ages of nestlings and the actual measurements on which it is based are presented in Table 6. Although the smallest tarsal measurement for an entire litter averaged 20.3 millimeters (Table 5), these cottontails were presumably at least 10 hours old. If this was true, the tarsal measurement at birth was about 19 millimeters or less. The tarsi of seven embryos averaged more than 16 millimeters.

In no case were the eyes of an entire litter found to open on the same day, and usually a period of 2 days was required for the complete eye-opening of an individual. The eyes of some nestlings began to open on the sixth day, when the tarsal measurement was approximately 31 millimeters; more often 7 days were required before these organs began to open (Table 6). Usually the eyes of the entire litter were completely open by the eighth day.

TABLE 6

COMPARISON OF AGE, TARSAL GROWTH, AND DEVELOPMENT OF NESTLING COTTONTAILS

Days old	Actual tarsal measurements	Remarks	Working scale to determine ages
At birth	mm.		mm. 19
1			21
2	22.5		23
3	24.5		25
4	26.7		27
5	28.4		29
6	30.0	Eyes begin to open	31
7	32.3	Eyes begin to open, or are open	33
8	34.2	Eyes open	35
9	36.0		37
10	38.0		39
11	40.0		41
12	42.3		43
13	44.7		45*
14	Had left nest		47*
15			49*
16			51*

* May leave nest.

PARENTAL CARE

Nestling cottontails usually received little maternal care, as no female was ever known to remain with her nestlings except at feeding periods. Guardianship of the nest apparently varied with individual females. Although each nest was visited daily and at varying times by the observer, generally speaking,

adult cottontails were not seen in the vicinity. At a few nests, however, the female was always seen and at others she was often present. When the female maintained a close watch over the young, the squeal of a nestling (usually resulting from the weighing or measuring procedure) often caused the mother to leave her form and approach within a few feet of the observer. One female ran to the nest three times while the young were being examined. Trippensee (1934) has cited examples of cottontails responding to the squeals of the nestlings in order to defend them from various predators.

TABLE 7
CAUSES OF NESTLING MORTALITY IN 1940

Mortality factor	Number of nests destroyed
Mowing	2
Excessive water	2
Undetermined mammal	2
Undetermined	2
Cat	1
Man	1
Plowing	1
Total	11

Proof that female cottontails move their nestlings to other locations is yet lacking, although evidence implying that this occurs has been obtained several times. Desertion appeared unknown to the cottontails, for the practice was suggested at only one nest—and here it appeared more likely that the female had been killed. Although the following situation was exceptional, it showed the amount of disturbance a cottontail endured to rear her young. A nest containing 2- to 3-day-old nestlings was found between a path and a large holding pen at the Loyalsock Experiment Station. The nest was about 1½ feet from the edge of the path, which was in continuous daily use. The young were measured and weighed daily by one of the writers and were just as frequently disturbed by other workers. Three days after the nest was found, a ditch—2 feet wide and 4 feet deep—was dug where the path had been. Before the construction of the ditch, a stake was placed at the nest and the workmen were informed of the nest's presence. For 10 days the female crossed the ditch to get to the nest, and she attended the young until they left.

NESTLING MORTALITY

Farming operations, mammalian predators, excessive water, and man were responsible for the destruction of 9 of the 35 active nests under observation. The young from two more nests disappeared before their eyes had opened, and the destructive agent could not be determined. Table 7 shows the causes of nestling mortality in the 35 functional nests under observation.

Besides the nests studied by the writers, 18 destroyed nests were reported by reliable persons. Table 8 shows the agents responsible for the mortality.

TABLE 8
REPORTED CAUSES OF NESTLING MORTALITY IN 1940

Mortality factor	Number of nests destroyed
Haying operations	6
Plowing	5
Man	3
Dog	2
Cat	1
Cultivation	1
Total	18

Tables 7 and 8 indicate farming operations as the leading destructive factors in relation to nestling cottontails. Plowing, haying, and cultivating were responsible for the loss of 51.7 per cent of the 29 nests destroyed. Plowing was an important mortality factor only during the early part of the nesting season. Haying operations accounted for the loss of eight nests. Mowing generally was not injurious to nestlings because of the protection afforded by the nesting cavity, but three litters, almost ready to leave their nests and frightened from the cavity, were caught in the cutting bar. Five litters were destroyed when hayrakes exposed or pulled the young from their nests, but usually the rakes passed over nests without harming the young. Three nests under observation were successful although both a mower and rake had passed over them. One nest in a cornfield was reported destroyed when the crop was cultivated.

Mammals were responsible for the destruction of 20.7 per cent of the 29 nests. Unknown predators, cats, and dogs, each destroyed two nests. No nests destroyed by avian predators were observed, doubtless because the nestlings were so well concealed.

Four nests were destroyed by man. The young were taken from their nests by persons who believed the mother had either deserted them or had been killed.

Excessive water destroyed two of the nests under observation. Nests were generally so well situated and constructed, however, that the young were warm and dry even after hard rains. Only during severe storms is any appreciable loss of nestlings likely because of drowning or wetting.

Beule (1940) reported a number of nestlings infested with larvae of the flesh-fly, *Wohlfahrtia vigil*, during the nesting season of 1939. This parasite was not found affecting nestling cottontails during the 1940 nesting season.

The success ratio of the 35 nests under observation was 68.6 per cent, or slightly greater than the 64 per cent of 1939 (Beule, 1940).

The success or failure of 81 old nests was determined by using the pellets of the nestlings as an index. The lining of each nest was carefully searched for pellets dropped by the young a few days before they left the nest. When pellets were found, the nest was considered successful; nests having no pellets were believed to have been destroyed. This search revealed that 60 of the 81 nests contained pellets, indicating the success of 65 per cent in 1940. The same procedure in 1939 showed a success of 64.7 per cent of 72 old nests (Beule, 1940).

SUMMARY

1. During 1940 cottontails nested from the middle of March through September.

2. May appeared to be the most important nesting month during the 1939 and 1940 breeding seasons.

3. Cottontails nested in a number of cover types; although most of the nests were found in open fields, this cover type did not have the greatest nesting density.

4. Apparently no particular density and height of cover were favored for nesting.

5. Favored nesting sites were found only in orchards, pine plantations, or woods.

6. Cottontail nests were found on all degrees of slopes from 0 to 35 per cent,

and the cavities usually faced downhill.

7. Nesting cavities were apparently dug and lined by the female rabbits, often several days before the birth of the young.

8. Nesting cavities were often abandoned, but active nests were not.

9. During the 1940 study, 35 litters of nestling cottontails and 9 sets of embryos were examined.

10. In 1940 the size of the average litter was 4.95, and in 1939 the average of 26 litters was 5.42. Litters during these 2 years ranged from 2 to 8 in size.

11. Litters were usually larger during the first half of the nesting season and became smaller as the season progressed.

12. Cottontails weighed about 25 grams at birth and averaged about 112 grams when they left the nest.

13. Tarsal measurement proved a satisfactory index of age of nestling cottontails. The daily tarsal-growth rate was about 2 millimeters.

14. The eyes of cottontails usually opened about 7 days after birth.

15. Nestlings normally left the nests 15 or 16 days after birth.

16. Except during feeding periods, nestlings received little maternal care.

17. Eleven of the 35 active nests under observation in 1940 were destroyed, and 18 additional cases of nest destruction were reported.

18. Farming operations were responsible for 51.7 per cent of the 29 nests destroyed.

19. Mammalian predators destroyed 20.7 per cent of the 29 nests destroyed, but no avian predation in cottontail nests was observed.

20. Excessive water may sometimes be an important mortality factor.

21. The success ratio of 35 active nests in 1940 was 68.6 per cent; in 1939, 64 per cent.

22. Pellets of nestling cottontails appeared to be a good index of the success or failure of old nests.

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INCOME POSSIBILITIES FROM A SMALL ARTIFICIAL POND IN EASTERN CONNECTICUT[1]

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The upland of Connecticut is a typical glaciated region with many small swamp and seepage areas at or near the divides between the principal streams. Fed by the run-off from these water reservoirs, the relatively short primary streams are fairly steady flowing. Early colonial industries made use of their waterpower wherever it was possible to develop a small pond and install a water wheel. These ponds have almost entirely disappeared although the foundations of many dams are still to be seen. Much of the agriculture also disappeared and open land has been replaced by forests. Modern transportation has made possible the reoccupation of much of these uplands as part-time farms or as year-round residences for city wage earners. Water areas are again becoming important as additional attractions to land areas, for their aesthetic or their recreational values.

This brings up the question whether it is possible to obtain revenue from such waters in a way that will not detract from their original value to the owners, or that may justify their existence for some other purpose than the pleasure derived from them.

The erection of a small dam in 1922, flooding a seepage area on the campus of the University of Connecticut, offered an opportunity to study the productive possibility of such a pond; the study was not begun, however, until nine years later.

The area flooded, known as Mirror Lake, was a wet-meadow seepage area that had probably been mowed for bog hay for the previous 100–150 years, through which flowed a small stream having a width of two to three feet and a depth of from one to four inches. This stream originates in two swampy areas of small extent within half a mile of the dam site and flows to the east into the Fenton Valley. The flow continues throughout the driest of years, but in much diminished volume. The dam erected is of concrete backed by earth, is some 300 feet long, and impounds an area of 4.7 acres within which is one small island, four-tenths of an acre in area. The maximum depth is about six feet but more than half of the area is less than three feet in depth. The original seepage area emerges from, and extends 50 to 100 feet beyond, the shore line in two places, having 325 and 425 feet of shore line, respectively, while the remaining 600 feet of shore line is firm and consists of well-drained upland soil. The island has a margin of 300 feet, mostly upland type. It has an elevation of about five feet above the surface of the pond and was planted with white pine, and white and Norway spruces. The stand is dense and forms excellent cover. A trunk-line highway parallels the eastern shore of the pond within 100 feet of the shore line. A dwelling house on this side is within 25 feet of the shore. At no point is the shore more than 300 feet from a surfaced highway, and there

[1] Part of the detailed information upon which this paper is based was collected by students in the Department of Forestry and Wildlife Management of the University of Connecticut.

are 19 residences, one store, and a garage within 400 feet of the pond.

Flooding, of course, immediately initiated a new ecological succession. The original mammals—meadow mice—apparently retreated to the island and from ocular evidence were extremely abundant during the first summer and autumn; but with freezing of the pond, the population was brought to normal by emigration or by the depredations of house cats. Muskrats moved in at an early stage and have been permanent residents. Neither minks nor mink signs have been reported, possibly due both to the small size of the brook and to lack of systematic observation. The area is very favorable to the development of bullfrogs which have maintained their numbers in spite of a considerable take each season.

There seems to have been a very rapid growth of fresh water mussels in the deeper portion of the pond. The original stock must have been in the brook as none were introduced. To the original minnows of the brook the Connecticut State Board of Fisheries and Game added perch, bullheads, crappies and sunfish in 1923. The present heavy goldfish population is from stock that escaped from the University Grounds Department fish ponds. The original meadow vegetation, as indicated by a study of the present marginal plants, was composed of from 30 to 35 species common in the locality.

This pond developed naturally for the first few years. Fishing was, for the most part, done at night, day fishing not being permitted. The muskrats were trapped by students working their way through the college. At rare intervals ducks of various kinds paid the pond transient visits but the pied-billed grebe was the only species that remained for any length of time. Various species of the heron family as well as ospreys were fairly numerous during the summer.

In 1932 a study was begun of the productive capacity of the pond in terms of fur and waterfowl, but no attempt was made to evaluate the fish resources. The original stock of fishes had thrived, however, and occasional large specimens were noted. Yellow perch up to 15 inches and crappies up to 12 inches were taken. There was abundant food available for predator fish if the number of sunfish, goldfish, and crawfish could be taken as an index. Only a short time previous to the discontinuation of the study, a plan for regulated fishing was accepted, and was in operation sufficiently long to show favorable results.

The original concrete dam was not made of the best of materials and in places its foundation was too shallow. The face of the dam was vertical; it received very considerable ice pressure during the winter, and by 1936 began to show serious leaks at the base and to disintegrate at the top. This caused an accelerating rate of seepage during the summer with increasingly longer periods of low water. The badly weakened dam partly went out during the winter of 1939–40, lowering the pond level at least a foot. A large amount of grading within the campus watershed caused rapid silting along certain sections of the shore line, which still further changed the volume of water and the shore line topography. For these reasons the study was terminated as of 1940.

No records are available for the fur take previous to 1932. However, an individual trapper reported that more than 40 pelts had been taken each season for several years. As to whether this

was the total there is no way of checking. The trapping did not take into consideration the leaving of breeding stock as the trappers were interested only in the immediate returns. It is, therefore, safe to assume that the pond had been intensively trapped each season up to the beginning of this study. Since then trapping has been limited to the shores of the pond, no traps being set on the island.

The flooding produced a pond site that has been occupied naturally and almost completely by water weed (*Elodea*), cattails, burreed, bulrushes, pondweeds, and pickerel weed, to which have been added a number of ornamental waterlilies.

The emergent vegetation, as cattails and burreed, has been largely restricted to the borders of the seepage areas, being scanty or absent along that part of the shore formed of upland soil. It has been an annual custom to mow all tall growth adjacent to, or within wading distance of, the shores of the pond. This is usually done during August.

Street lights cast reflections on the pond, making possible a certain amount of observation of the night activities of muskrats. Signs of preparation for winter are usually evident about the first of September when relatively stable feeding platforms such as rocks, bogs, and clumps of brush or stumps are selected and food beyond present needs is collected. These platforms are used year after year and are, for the most part, adjacent to the seepage areas. As cold weather approaches, more food is collected into sizable piles. The principal material used is *Elodea*, in bunches about the size and shape of shredded wheat biscuits. Other bottom material such as clam shells, mud, bits of wood or other movable objects are frequently used. These piles develop into the winter houses. In general, the use of cattails is limited, possibly because of the mowing in the late summer. There is an underwater entrance provided for winter use. The preferred water depth seems to be two feet more or less. As a house approaches the common maximum size, new houses are started at less favorable sites and this continues until the water freezes. The *Elodea* has very little body and the houses cave in during late winter thaws, and by the middle of spring almost entirely disappear.

Extensive bank burrows were constructed where the slope was sufficiently abrupt. These became quite elaborate and paralleled the ground surface just below the turf roots and were almost always provided with two entrances. In the course of time they caved in and were either abandoned or patched by filling in the breaks with the same materials that were used for the lodges. In one case a lodge was built over such a break at a distance of about ten feet from the pond. As the more abrupt banks became worked out, there was a tendency to use the higher portions of the seepage areas but these burrows were subject to flooding during high water. The island was the only place where both burrows and lodges were built consistently and in close proximity. During thaws the animals used the margins of holes in the ice as feeding platforms. Often food—apparently *Elodea*—accumulated at such points and might be eaten later if an animal felt so inclined after taking a sun bath.

Normal drouths expose the entrances and bank burrows during the latter part of the summer without reduction of the fall stock.

The break in the dam lowered the water level, entirely exposing the entrances of the bank burrows throughout the year. This apparently produced conditions undesirable for breeding. The population during the summer of 1940 was very low and built only three small houses in the fall. It would seem advisable to hold pond fluctuations to a minimum, especially during the early breeding season.

No satisfactory method of inventory of the total population was found. The take of fur has been determined arbitrarily and at no time have traps been set on the island. The population is free to migrate at all times, and, as stated before, had been subject to unregulated trapping up to the season when the experiment was started. Therefore, there was no "built up" initial stock.

MUSKRAT HOUSES AND NUMBER OF PELTS TAKEN, 1932–1940

Year	*Large houses*	*Pelts taken*
1932–33	11	32
1933–34	13	35
1934–35	23	37
1935–36	17	25
1936–37	5	7
1937–38	10	12
1938–39	13	24
1939–40	3	13
Total		185

This shows a yearly average of 23.1 pelts. Activities of the muskrats during the fall of 1935 indicated a very abundant population. The trapping limit, however, was set at 25 with the idea of increasing the population, if possible. Trapping was in February and early March, 1936, and there were apparently more than the average number of animals, as there were many cut skins that seemed to have resulted from fighting. In spite of the leaving of more than the average number at the end of the trapping season that year, very few animals were in evidence during the summer of 1936, and few lodges were built during the next fall. Simultaneous drops of muskrat populations were reported in other parts of the state. The catch on the pond was reduced to seven animals in order to see if the population would build up. Fluctuations already observed, however, seem to have had little relation to the breeding stock. The population at the time the experiment was begun was that surviving a number of years of unrestricted trapping, yet it was apparently as high as that of 1938–39, the last year of complete records. Consistent with the maintenance of sufficient breeders, it is doubtless safe to take all animals possible from the shore of the pond, provided no traps are set on the island. That this policy can be carried out is probably due to the free movements of muskrats to or from adjacent waters.

Study of some 75 animals showed the average to be 1,260 grams in weight and 569 mm. in total length. The largest male weighed 1,930 grams while the largest female weighed 1,560 grams. The smallest animal trapped—a female—was 792 grams in weight. One albino was taken; it had pink eyes, white skin on the feet and tail, and pale fur. Its size was about normal.

The average size of these pond animals is well above that of brook muskrats and it is safe to place the value of the average pelt at one dollar, indicating an income from the fur take of $23 per year, or an annual return of six dollars per acre from this old bog meadow converted into a pond.

Arrangements were made in 1934 whereby Dr. Miles D. Pirnie of the Kellogg Wild Life Sanctuary in Michigan

sent us six wild mallards—two drakes and four ducks. These were pinioned and liberated on the pond. The birds bred and in the fall there were 17. Drainage from the basement of the greenhouse maintained a small area of open water throughout the winter, and feed was provided as necessary.

The second season the birds began to spread to adjoining nesting areas. Two resident drakes seem to be about the maximum for this pond. They will hold as many ducks as possible, varying from one to three each. The favorite nesting place was under the branches of the spruces on the island.

Mortality was high. Of 52 eggs laid only eight survived in 1935. The cause of mortality was not determined. However, one year there were 54 newly-hatched ducklings on a Saturday; a week of cold, northeast wind and rain left only three survivors the next Saturday. There seemed to be much better survival of broods hatched after June 1 than of those of earlier dates. The resident population built up each November as the birds that had nested on adjacent waters came in. The high point was during the winter of 1937–38 when 51 mallards were in common residence. Twenty-three were trapped by the State Board of Fisheries and Game and liberated at the Shade Swamp Sanctuary in the spring of 1938.

Drainage of the warm water from the greenhouse was diverted and the area of open water during the winters of 1939–40 and 1940–41 was much less. The birds have shown a tendency to leave the pond for periods as long as two weeks but have returned each time. The average population has been from 30 to 40. An unknown number have been shot during the open season on waters away from the game preserve. There has also been some poaching at the winter feeding area. The total feed approximates three bags of scratch feed per season. It would seem that an annual crop of not less than ten mallards could be taken. The ducks also add much to the attractiveness of the pond.

The water lilies of cultivated varieties have thrived and apparently are not on the preferred food list of the muskrat. Blooms and planting stock for sale might well furnish an additional income.

As stated before, the fishing has not been evaluated but it could well supply a certain amount of food and recreation.

The Farm Management Department of the Extension Service states that a bog area of this type is a liability on the modern farm and requires annual expense to keep it from becoming an eyesore. However, a typical area of such land when flooded produced the following crops which have a cash, or a personal satisfaction, value, or both.

In fur from muskrats, 23 pelts at $1 each	$23.00
In mallard ducks, 10 at $1 each	10.00
In frogs, about 100 large frogs, 20 lbs. at $.40 per lb.	8.00
In fish, abundant for family	5.00
In fishing, personal recreation or paid by hour	?
In pond lilies, personal satisfaction	?
In pond lily blooms and planting stock for sale	?
	$46.00, plus

This represents a conservative estimate of not less than $10 per acre annual return for crops that are in demand and for which a minimum of labor is required in harvesting. In all probability this income would respond to increased intensity of management, and represents more nearly the minimum than the maximum obtainable.

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TROUT MANAGEMENT STUDIES AT GREAT SMOKY MOUNTAINS NATIONAL PARK

Willis King

The Great Smoky Mountains, lying between the Pigeon River on the east and the Little Tennessee on the west, contain some of the finest trout streams in the Southern Appalachians. All rise under high ridges, and eventually reach the waters of the Tennessee. The clear waters of Little River, West Prong of Little Pigeon, Cataloochee Creek, Straight Fork of the Oconalufty, Deep Creek, Eagle Creek, and many lesser streams are as musical as their names are appealing. These living waters of the Great Smokies provide not only the most delicate of foods for the angler's creel, but offer a type of recreation that is all too rare. It was to develop and preserve this natural resource that fisheries studies were undertaken, the results of which are presented in this paper.

Physical Features of the Streams

The gradient of descent varies from 2 to 20 per cent, averaging in the streams covered by this study from 3 to 8 per cent. The stream beds are principally of large boulders and rubble. Only Abrams Creek has a bed at least in part of shelving rock. The stream flow is relatively stable and critical conditions exist only at infrequent intervals. Plates 9 and 10, respectively, show Little River at one of its highest flood periods and again during the low water of the autumn of 1939. When the photograph for Plate 10 was taken, the rate of flow was 21.2 f. s., probably less than half the normal flow. High water, which comes suddenly and with sufficient force to move large boulders in the stream bed, is certain to affect adversely fishes and other aquatic organisms. Low water on the other hand concentrates the trout of all sizes, the minnows, darters, and other free-swimming species within the larger holes where predation and cannibalism are rife. Should the low water come while temperatures are in the 80's, loss of trout is certain to result. Fortunately in the Great Smokies the streams are at their lowest in the autumn when cool nights and short days keep water temperatures at favorable levels. In prolonged zero weather the streams may become largely frozen (Plate 11) and the flow reduced, but no distress of trout has been noted under this condition. There is very little aquatic vegetation in the upper portions of the streams and the rapid fall gives little opportunity for planktonic organisms to develop. The aquatic fauna then is limited in quantity if not in variety. Quantitative studies, other than those made by the Bureau of Fisheries survey party in 1934 (Burrows, et al, 1935) have not been made. The prevailing rocks are sandstone, conglomerate, schist, shale, and other acidic types, except in a small part of the Abrams Creek watershed where limestone and dolomitic outcrops occur. The water is usually acid, except in the lower portions of the streams where it approaches neutrality. A deficiency in basic carbonates is undoubtedly a factor limiting the growth of fish foods and possibly of the fishes also. A

chemical analysis of the waters of Kephart Prong, a tributary of the Oconalufty system, is given in the Progressive Fish Culturist No. 29 (King, 1937a). These natural factors are beyond control and limit the total aquatic life, including game fishes, that it is possible to maintain. Fortunately, however, carefully protected forests and abundant bank cover greatly moderate natural fluctuations in rainfall and temperature.

ORGANIZATION OF THE CREEL CENSUS

Practically all streams in Great Smoky Mountains National Park support trout. Many of the larger streams are accessible by road and nearly all can be reached by foot or horse trails. The traffic system around and within the park makes the lower reaches of the streams the most accessible, while many of the headwater tributaries are in a wilderness. High confining ridges establish definite points of ingress and exit from many of the watersheds. Then, too, the truck trails that usually follow the larger streams quite closely are closed to public travel at places sufficiently near the park boundary that creel census stations can be located at strategic places. On the streams selected for this study, natural topography, aided by administrative regulations, requires that all fishermen using the streams pass by the creel census stations. Since CCC facilities were employed, the availability of enrollees for the work was also taken into consideration in selecting the streams for investigation. On the Tennessee side, Little River above Elkmont was studied in 1938, 1939, and 1940, and Abrams Creek in 1940. Several of the streams on the North Carolina side also were suitable for a creel census, Big Creek and Straight Fork being used in 1938, these two and Forney Creek in 1939, and Straight Fork, Forney Creek and Cataloochee Creek in 1940. (See Tables 1, 2, and 3.) Findings of a census taken on Deep Creek and Forney Creek in 1935 are also reported (Table 7).

The creel census was organized to gather information that might indicate desirable changes in management policy; but specifically to obtain definite figures on the legal catch removed from the streams, the number of smaller trout taken and returned to the water, and to learn the extent of use of the streams by out-of-state visitors. There are few published data on the fish population and management of trout streams in the Southern Appalachians. King (1939) reported on the distribution of brook and rainbow trouts in the Great Smokies, and Keil (1939) recorded the findings of studies in the Pisgah National Forest, which offer opportunity for comparison with those in the Great Smokies.

Keil showed that the average catch of legal-sized trout in the Pisgah Wildlife Management Area was 3.70 fishes in 1938. In the Great Smokies, the average (mean) catch per angler on the streams studied in 1938 was also 3.70 fishes, in 1939 it was 4.06, and in 1940, 3.92. He reports that approximately 6,000 undersized rainbows were hooked and released to 2,226 legal-sized ones retained —a ratio of one kept to 2.6 returned to the water. This compares with one legal trout to 4.6 undersized fishes reported in the Great Smokies in 1938, one to 3.84 in 1939, and one to 1.53 in 1940. Keil records the average length of the

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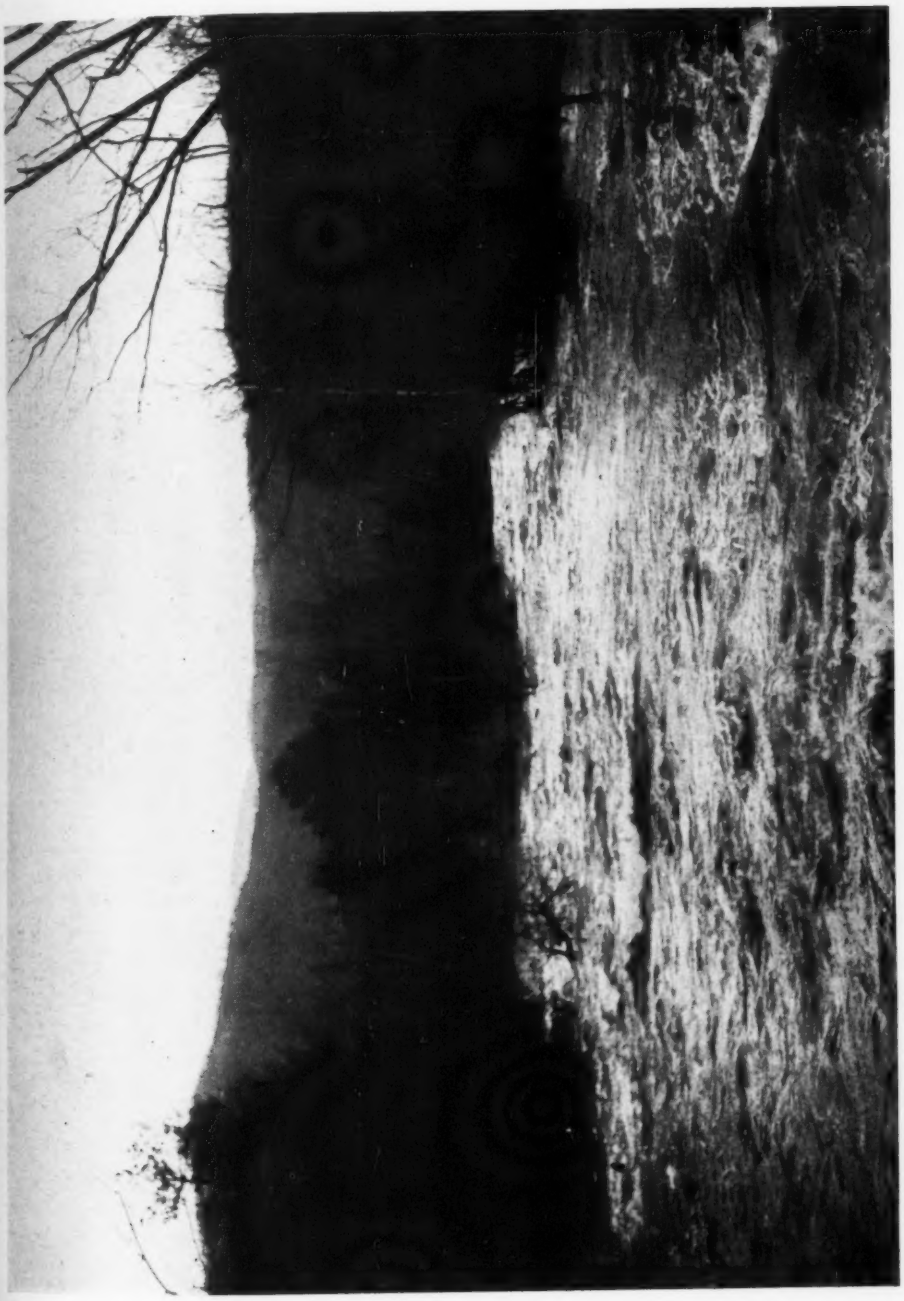
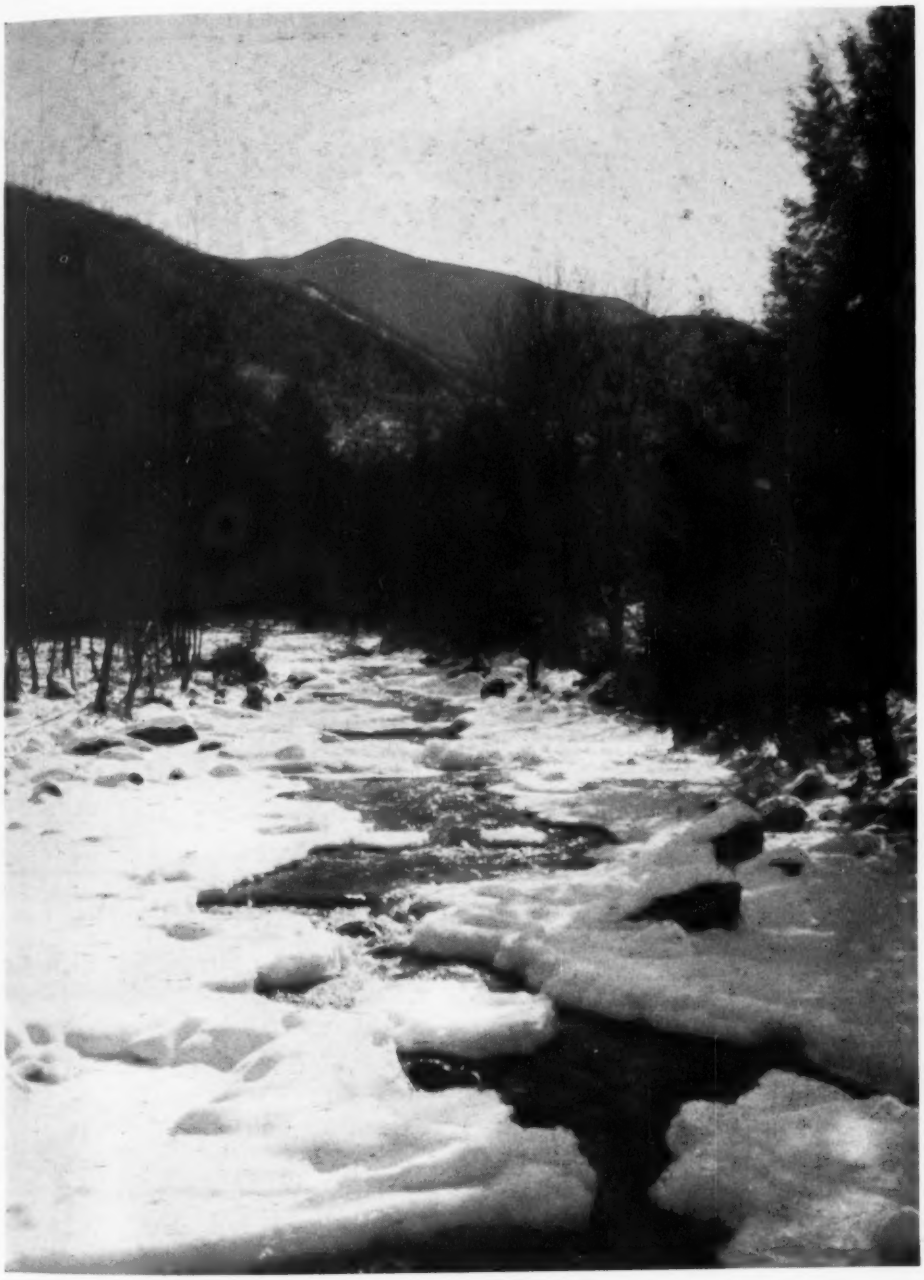


Little River, looking downstream from Elkmont, during the high water of March 24, 1936. The stream was higher at this date than at any other from 1934 through 1940.

Taken from the same spot as Plate 9. This shows the lowest water condition observed on Little River from 1934 to 1940. Photo taken October 26, 1939.



Looking upstream from the same spot where Plates 9 and 10 were taken. The reduction of flow and extensive formation of ice are clearly evident, following a period of sub-zero weather. Photo taken January 23, 1940.

A twenty-two inch rainbow from the Great Smokies taken in August, 1937. This fish weighed approximately 3 pounds, and was in its sixth summer.

A twenty-two inch rainbow from the Great Smokies taken in August, 1937. This fish weighed approximately 3 pounds, and was in its sixth summer.

trout taken in the Pisgah Game Preserve in 1938 as 8.512 inches. The average size (mean) of the legal trout reported from all the streams surveyed in the Great Smokies varied from 8.33 to 9.82 over the three-year period. Averages were not extended to the undersized fishes because of probable inaccuracies in reporting the number and the difficulty of arriving at a true class mean. It is apparent that the fundamental problems of fisheries management in the Pisgah National Forest and in the Great Smoky Mountains National Park are similar and that some of the same management procedures are applicable to both regions.

CREEL CENSUS RETURNS

The returns from the streams studied are summarized in Tables 1, 2, and 3. Table 1 gives the annual summaries for all streams on the North Carolina side and for Little River in Tennessee in 1938 and 1939. Tables 2 and 3, of Little River and Abrams Creek for the 1940 season summarize the returns by month to illustrate seasonal fluctuation in fishing effort and catch. The total catch from streams varied considerably due to several factors, principally accessibility, size, and past management, including the stocking program as well as the trout foods available. Little River because of its accessibility and adaptability to management procedures was given special attention. This stream is the largest covered by this census and has long been known as a good trout-producing stream. It will be noted from Tables 1 and 2 that the catch per hour was 1.05 in 1938, 1.22 in 1939, and 1.32 in 1940, while the number of legal trout taken per mile was 380, 471.5, and 1,167.5 respectively for the same years. Returns from Little River illustrate the value of stocking with legal-sized trout prior to and during the open season. The ratio of legal to undersized trout was considered satisfactory in 1938 and 1939 reports, but it seemed that the average catch could not be appreciably enlarged by increasing the number of fingerling trout liberated in the autumn. Trout of all sizes were in fair to average condition according to their weight-length ratios, and undoubtedly were utilizing practically all available natural food. Autumn stocking was eliminated in 1939 and instead 1,600 rainbow and 500 brook trouts, all legal size, were liberated in late April and early May of 1940. All of the brook trout and 500 of the rainbows were marked by punching an oval hole one-fourth by three-eighths inches in size in the caudal fin. The brook trout retained a recognizable hole or scar at this place, but the rainbow either tore out the hole or obliterated it by regeneration in a few weeks. Approximately half of the released brook trout were taken in the first 8 weeks of the season. The last week in July, 1,010 rainbow and 521 brook trout, all legal size, were stocked in the same water. These fishes were all marked by clipping the right pelvic fin. This type of identification proved reliable for both species during the remainder of the season. Records show a return of 678 of the rainbows and 337 of the brook trout by the last of August. This is a return of 67 per cent of those released. It will be noted that marked rainbows made up only 25 per cent of the catch of that species in August, while the marked brook trout contributed 67 per cent of all of that species taken. The stream is more favor-

TABLE 1

SUMMARY OF CREEL CENSUS RETURNS, GREAT SMOKY MOUNTAINS NATIONAL PARK, 1938 TO 1940

Size in inches	Species	Big Creek		Cataoolchee Creek	Straight Fork			Forney Creek		Little River	
		1938	1939	1940	1938	1939	1940	1939	1940	1938	1939
Under 6 inches	rainbow	16,859	4,442	2,292		1,594	2,339	5,384	3,190	8,702	3,336
	brook		186	87		161	82	95	36	155	304
6 to 7.9 inches	rainbow	2,249	4,391	1,266		3,110	276	1,651	277	3,976	4,672
	brook		154	66	407	123	225	22	94	13	136
8 to 9.9 inches	rainbow	1,756	1,708	1,404	1,184	805	596	1,069	922	3,599	3,395
	brook		48	21	42	70	59	9	31	1	37
10 to 11.9 inches	rainbow	111	24	318	222	39	126	66	68	157	167
	brook		2	21	11	8	29	4	1	1	1
12 to 13.9 inches	rainbow	87	6	65	20	2	8	1	12	29	10
	brook			6	1	1	2				
14 to 15.9 inches	rainbow	1		9	2	1				1	6
	brook			1			1				
16 inches and over	rainbow	1	2	7	3						
Total undersized trout	rainbow	19,108	8,833	3,558		4,704	2,615	7,035	3,467	12,678	8,008
	brook		186	87		161	82	95	36	155	304
	both	19,108	9,019	3,645	2,938e	4,865	2,697	7,130	3,503	12,833	8,312
Total legal trout	rainbow	1,877	1,740	1,803	1,431	837	730	1,136	1,002	3,785	3,578
	brook		204	115	461	212	316	35	116	15	194
	both	1,877	1,944	1,918	1,892	1,049	1,046	1,171	1,118	3,801	3,772
Total anglers reporting		634	407	587	397	297	256	440	388	1,016	812
Total hours expended		3,037	2,111.5	3,132.5	2,294	1,765.5	1,204	2,244	1,811	3,625	3,080
Average creel		2.96	4.77	3.26	4.76	3.53	4.08	2.6	2.87	3.74	4.64
Legal trout per hour's fishing		.62	.92	.61	.83	.58	.86	.52	.62	1.05	1.22
Legal trout per mile of stream		312.8	243	348.7	315.3	174.8	298.8	146.4	203.3	380	471.5
Undersized trout per mile		3,184.6	1,127.4	662.7	472.5e	811	771	891.2	636.9	1,283.3	1,039
Miles of stream covered by the census		6	8	5.5	6	6	3.5	8	5.5	10	8
Ratio of legal to undersized trout		1:10.2	1:4.6	1:1.9	1:1.5	1:4.6	1:2.58	1:6.1	1:3.13	1:3.4	1:2.2
Average size (mean) of legal trout		8.89	8.51	8.57	8.48	8.48	8.41	8.69	8.77	8.71	8.63

Note: The upper broken line separates the undersized from the legal sized. All measurements are total length in inches.
e: estimated from partial returns.

TABLE 2

SUMMARY OF CREEL CENSUS RETURNS FOR LITTLE RIVER, 1940

(Approximately 5½ miles of stream covered by the census, from the gate above Elkmont to the mouth of Meigs Post Prong.)

Size in inches	Species	May 16–31	June	July	August	Totals
Under 7 inches	rainbow	2,452	2,104	1,019	1,420	6,695
	brook	85	54	40	171	350
7 to 7.9	rainbow	668	618	482	512	2,280
	brook	142	63	84	121	410
8 to 8.9	rainbow	589	615	424	595	2,223
	brook	52	20	58	129	259
9 to 9.9	rainbow	204	290	236	244	974
	brook	7	2	29	17	55
10 to 11.9	rainbow	45	50	48	51	194
	brook		1	1	4	6
12 to 13.9	rainbow	5	4	4	7	20
Total legal trout	rainbow	1,511	1,577	1,194	1,409	5,691
	brook	201	86	172	271	730
	both	1,712	1,663	1,366	1,680	6,421
Total undersized trout		2,537	2,158	1,059	1,591	7,045
Number anglers		334	483	311	318	1,446
Number hours expended		1,225	1,506	984	1,124.5	4,839.5
Average creel		5.12	3.23	4.39	5.28	4.30
Average legal trout per hour		1.40	1.10	1.39	1.49	1.32
Average legal trout per mile		311.27	302.36	248.36	305.45	1,167.45
Ratio of legal to undersized trout		1:1.48	1:1.30	1:.77	1:.95	1:1.1
Marked trout returned		B, 147	B, 63	R, 356 B, 150	R, 322 B, 187	R, 678 B, 547
Average size of legal trout		8.23	8.35	8.38	8.22	8.33

able to rainbow trout, and brook trout succeed only in the upper mile of the water opened to fishing. This return of marked trouts compares favorably with that found by Hazzard and Shetter (1938) for Pine River in Michigan. They report a weighted average return from planting legal-sized brook trout of 19.8 per cent and for rainbows of 17.5 per cent.

The legal trout stocked in Little River were thoroughly scattered throughout the open water so that there was in no place a concentration of fish large enough to be detected. At first the stocked individuals were not as wary as their wild companions, but within a period of about two weeks they were no more easily observed or taken than the wild fish. The rearing pools in which these fishes were grown are in an isolated location and the fishes are some-

TABLE 3

SUMMARY OF CREEL CENSUS DATA, ABRAMS CREEK, 1940

(Approximately 3½ miles of water from the junction of Forge and Anthony Creeks to the falls of Abrams Creek, were open to fishing and covered by the census. All measurements are total length in inches.)

Size in inches	Species	May 16–31	June	July	August	Total
Under 7 inches	rainbow	829	218	238	451	1,736
7 to 7.9	rainbow	81	39	41	29	190
	brook	16			25	41
8 to 8.9	rainbow	229	84	36	49	398
	brook	4			39	43
9 to 9.9	rainbow	250	84	25	42	401
	brook	9			26	35
10 to 11.9	rainbow	190	73	48	42	353
	brook				1	1
12 to 13.9	rainbow	76	23	28	24	151
14 to 15.9	rainbow	18	7	11	6	42
16 and over	rainbow	1	7	8	7	23
Total legal trout	rainbow	845	317	197	199	1,558
	brook	29			91	120
	both	874	317	197	290	1,678
Total anglers		170	81	60	79	390
Total hours expended		1,065	480	404	525	2,474
Average creel		5.14	3.91	3.28	3.67	4.30
Average legal trout per hour		.82	.66	.49	.55	.68
Average legal trout per mile		250	90	56	83	479
Ratio of legal to undersized trout		1:.97	1:.68	1:1.21	1:1.55	1:1.03
Average size of legal trout		9.76	9.86	10.3	9.57	9.82

what wild even there. Apparently wildness can be controlled to a considerable extent by the type of pool employed in holding trout over winter and by the methods of feeding and handling. Proper selection of foods and the use of more natural pools and raceways will do much to add color to the hatchery-raised trout and make them more desirable for the angler. One thing in favor of the hatchery-raised fishes was that they were considerably heavier than wild fishes of the same length. Numerous observations and reports of anglers were to the effect that many of the larger trout recently liberated from the rearing pools broke water more readily after being hooked and for fish of their length put up a strong battle. The increase in legal fish taken per mile in 1940 can be traced to two factors, one the change in stocking policy outlined above and the other, a

TABLE 4

TROUT STOCKING RECORD, 1935, TO THE CLOSE OF THE FISHING SEASON, 1940, ON CERTAIN OF THE STREAMS WHERE CREEL CENSUS RETURNS ARE GIVEN

(Including all trout stocked above the creel census stations, even in tributaries which in many instances are not opened to fishing. Weight is in pounds and size is in inches.)

Stream	Year	Season	Rainbow	Weight	Size	Season	Brook	Weight	Size
Big Creek	1935	C	2,000		4–9				
	1936	C	4,000		3½				
	1937	C	9,555	150	3½				
	1938					C	1,500	61	5
Straight Fork	1936	A	9,000		3				
	1936	B	13,500		3				
	1936	C	2,250		4				
	1937	C	4,850	80	4	C	10,325	206	4
	1938	C	4,750	50	4	C	9,490	150	5
	1939	C	1,300	50	6	C	4,156	151	5
Forney Creek	1936	C	8,300		4				
	1937	C	19,250	236	5	C	10,845	125	3
	1938	C	22,700	200	3	C	7,250	100	4
	1939	C	7,912	164	4–5	C	1,900	60	5
Little River (above the creel census station)	1935	B	8,500		2–4				
	1936	B	18,200		2–6				
	1937	C	8,193	133	3–5	C	7,800	153	3–5
	1938	C	3,500	100	3–6	C	8,030	191	3–6
	1939					C	4,004	100	4–6
	1940	A	1,600	245	7–8	A	500	75	7–8
	1940	B	1,010	156	7–8	B	521	106	8

A, stocking done in April and May prior to opening of the fishing season, May 16.
B, stocking done during the open season, May 16 to August 31.
C, stocking done after the close of the fishing season in September, October, and November.

lowering of the size limit to 7 inches. Of the total catch of 6,421 legal trout, 2,690 were between 7.0 and 7.9 inches, constituting almost 42 per cent of the total catch. In former years trout of this size class were not available. A further check on this program will be possible after the returns of the 1941 season are known, and in addition information on the value of stocking legal-sized fish in the autumn will be available from returns from 1,000 rainbows and 500 marked brook trout stocked in September and October, 1940. The increase in the catch of "keepers" on Little River in 1940 received many favorable comments from anglers. From estimates based on creel census figures, corroborated by observations and reports from anglers, at least half of the available legal-sized trout were taken from the stream. Continued and more careful checking on this point will be necessary to determine just what proportion of the adult fish can be safely taken as an annual crop.

Abrams Creek offers an interesting contrast with Little River. This stream, as stated above, is the only one of appreciable size in the Great Smokies that flows chiefly over ledge rock and carries limestone in solution. It has a heavy population of snails, aquatic insects, and crustaceans, and contains more veg-

etation than any other stream in the Great Smokies. Trout grow on the average from one-third to one-half again as fast in this stream as in any other, and although it is a hard stream to fish, some of the best catches are made in it. Smallmouthed bass are stopped by a falls at approximately 1,500 feet elevation, and above that, rainbow trout dominate throughout the main stream. The latter species was introduced about 40 years ago, and has provided fair to excellent fishing since. When the National Park Service acquired the land in 1937, the stream had been badly abused by seining, dynamiting, and bait fishing, and there had been no restocking for several years. The watershed is almost all virgin forest, and with protection the stream quickly recovered. It was closed to fishing in 1938 and 1939 and the tributaries and upper reaches lying in Cades Cove were stocked with 6-inch rainbows in the autumn of both years. Apparently most of these trout moved down into the main stream for they were clearly recognizable as the dominant size and age classes taken in 1940. A favorable food supply and an open environment enabled them to make an average growth of 3 to 4 inches a year, with apparently a very high survival. There were a few large rainbows in the stream when the Park Service took over its management, but almost no small ones. The increase can be definitely attributed to stocking and in this instance from stocking the tributaries rather than the main stream.

BROOK-RAINBOW TROUT RELATIONSHIPS

The importance of brook trout in the total catch does not appear great upon first inspection of the returns. Rainbow trout are dominant in at least three-fourths of the water open to fishing annually at Great Smoky Mountains National Park, and probably will hold that position indefinitely. Much of this water was originally occupied by brook trout (King, 1937b), but a combination of adverse conditions has considerably altered the original picture. Nearly all headwater streams above approximately 3,000 feet support the species, and also several lower streams that have barriers impassable to rainbows and where that species has not been introduced. In many instances the protection of the native brook trout and its attendant environment is of greater importance than its management on a yield basis. Many fingerling brook trout have been liberated where their sole purpose was to fill a niche in nature formerly occupied by their species and again available, because of recovery of natural environment.

Limited numbers of stocked brook trout together with still fewer wild fish, migrate downstream and are taken by anglers, but the number is not great. Experience has repeatedly shown that very little benefit has been obtained from stocking fingerling brook trout under six inches in length in water where rainbow trout occur. Some of those unfortunate enough to find themselves in the company of the rainbow promptly migrate upstream and the majority disappear within a year's time. On Indian Creek, a tributary of Deep Creek, a fall at the mouth of the stream prevents the further migration of rainbows upstream but the species was planted there at least a score of years ago and a few times since. Poor fishing was afforded,

however, and it was decided to attempt to restore brook trout. A total of nearly 30,000 brook trout fingerlings 3 to 6 inches in length were stocked in about 5 miles of stream from 1936 to 1939. In the autumn of 1940, a survey of the fish population, by observation and by hook and line, indicated that there were very few if any brook trout in the lower 3 miles of the stream, and that this species was dominant only above some low cascades near the upper end of the zone stocked. In fishing below these cascades, 20 rainbow to 2 brook trout were taken.

Other streams show more promising results. Straight Fork yields both brook and rainbow, wild and propagated, often from the same hole. Above about 3,000 feet elevation brook trout are numerous and soon assume dominance, while below that altitude, larger individuals are frequently taken along with rainbows. Bradley Fork presents similar conditions. The presence of 29 brook trout in the creels recorded for Abrams Creek, for May 16–31, is interesting. These were from a lot of 500 liberated a month earlier some three miles above in a tributary stream. In August, 91 brook trout were reported. These were stocked at or slightly above the point where taken, and were part of a lot of 200 put there July 30 to see whether or not they could survive at that low elevation (1,800 to 1,600 ft.) and in competition with adult rainbows in Abrams Creek.

Hoover (1939), in discussing the behavior of brook trout in New Hampshire streams, expressed the belief that they cannot be depended upon to leave feeder streams and headwaters as they grow older, and thereby contribute to better fishing in lower waters. He further stated that their downstream migration, if any, is not determined by age but probably by size attained, and is a reaction against limited space and water area of headwater streams. This seems to be equally true in the Southern Appalachians. The normal spread of the brook trout seems to be a gradual one and upstream to a greater degree than downstream. This has been clearly observed in several streams following stocking and in those with primitive populations as well. Rainbows on the other hand, have been observed to travel several miles both up- and downstream in a year's time.

Conditions in the Great Smokies are improving for the brook trout, but except in a few streams as those at higher elevations, and those free from rainbows, the release of fingerling brook trout does not seem to be an economical procedure. Spring stocking with legal-sized fish offers one solution to the problem of maintaining brook trout and the development of wild strains from the region is another. In National Park streams it does not seem advisable, at least at present, to undertake a program of poisoning to remove the present fish population in order to re-establish the brook trout. Nevertheless, since these trout are native to the park and rainbows are classed as exotic, the former species is favored, and stocked wherever the chances of success are considered favorable. The preservation of native stream species is considered more important than the production of a maximum catch. Brook trout have shown a more rapid rate of growth, greater freedom from disease, and are considered more easily handled than rainbows in rearing pools at Great Smoky Mountains National Park.

MEASUREMENTS OF TROUT

Tables 5 and 6 summarize data available on length-age and length-weight relationships. It is recognized in many instances that an insufficient number of specimens is reported to give real significance to the averages, but since nothing has been published to date on this phase of fisheries work in the Great Smokies, the data may have some interest. For a true comparison, a representative series should be taken from any particular stream within a 30-day period. Extremes in either age or weight relationships are likely to be encountered in any stream, and from the data used in compiling these tables there is indication of considerable differences in growth rate on different streams. Most of the specimens measured were wild fishes, taken from streams where no stocking had been done. The fastest growing fishes (hatchery-reared) came from Abrams Creek and the slowest from Big Creek. These streams are at opposite extremes of the Great Smokies.

TABLE 5

TOTAL LENGTH—AGE CLASS OF 324 RAINBOW TROUT

Total length in inches	Age Class							Totals
	1	2	3	4	5	6	7	
3.0– 3.9	2	1						3
4.0 4.9		2						2
5.0– 5.9		16	2					18
6.0– 6.9		23	28	2				53
7.0– 7.9		8	42	12				62
8.0– 8.9		4	36	10				50
9.0– 9.9			23	11	3			37
10.0–10.9			9	16	2			27
11.0–11.9			1	8	1			10
12.0–12.9			3	10	6			19
13.0–13.9				6	2	4		12
14.0–14.9				4	3	1		8
15.0–15.9				1	5	1		7
16.0–17.9					5	5	2	12
18.0–19.9						1	1	2
20.0–21.9							1	1
22.0–23.9						1		1
Totals	2	54	144	80	27	13	4	324

These fish were taken from streams in Great Smoky Mountains Park from 1936 to 1940. The number of annuli were determined with the aid of a binocular microscope under 40X magnification. Almost all the fish were taken between April 1 and the cessation of growth in the autumn and were classified by taking the number of annuli plus 1. Trout taken in late autumn and early spring will have the age class identical with the number of the last annulus.

It is interesting that no trout older than their seventh summer have been taken. Undoubtedly older fish do occur, but trout more than 18 inches in length are rare. Just what happens to the older and larger rainbows is still an unsolved problem. There is some evidence that many of them migrate considerable distances downstream in late autumn and reach an unfavorable environment from which they cannot escape. Adult rainbow trout have been taken at the mouth of Little River where it empties into the Tennessee, miles below the normal

lower limits of the species.

From an examination of the rainbow trout scales recorded in Table 5, it was apparent that the growth of the species slows down in September and practically ceases early in October. Low water in early autumn appears to contribute to a decline in feeding and growth. In 1939 an interesting observation was made in this connection. A very dry late summer and autumn that year reduced the streams to the lowest point observed since 1934. Fortunately the nights remained cool, and there was no loss of fish observed due to unfavorable water temperatures. A small series of trout taken from Road Prong, a tributary of West Prong of Little Pigeon, near the end of October, showed that growth had come to a standstill some weeks before, and had very recently been resumed. A few showers early in October had restored that particular stream to a near normal flow, and apparently the fishes had resumed feeding; a warm autumn favored activity. This phenomenon may recur under the right combination of conditions and confuse the investigator unless he happens to know local conditions at the time.

A series of 23 rainbow trout measuring from 5 to 8 inches in total length was taken from the Middle Prong of Little Pigeon River September 19, 1940, to check on their growth rate in that particular stream. All of the rainbows present in this stream are naturally-spawned fish, as a barrier constructed below the point of collection prevents their up-stream migration and the species has not been stocked above this barrier by the National Park Service. It was found that all rainbows of 6 inches or more in total length had well developed gonads and would have spawned either in the succeeding late autumn or early spring. One of these fish was completing its fourth season's growth, thirteen their third, and four their second season. The condition factors on this series of trout ran from 1.5 to 2.8, with 18 of them falling between 1.6 and 1.9 ($K = \frac{\text{weight in grams} \times 10^5}{\text{standard length}^3}$). In by far the majority of cases, wild fishes taken

TABLE 6

WEIGHTS OF 128 RAINBOW TROUT, CLASSIFIED ACCORDING TO TOTAL LENGTH

Total Length (in inches)	No. Specimens	Range in Weight (ounces)	Mean Weight	Standard Deviation
6.0– 6.9	31	1–2.4	1.8	±.8
7.0– 7.9	30	1.5–4.4	2.6	±.9
8.0– 8.9	19	2–4.4	3.3	±.6
9.0– 9.9	15	4– 6.4	5.4	±.65
10.0–11.9	13	4– 8.4	6.2	±1.1
12.0–13.9	8	8–13.9	11.1	±1.7
14.0–15.9	3	16–20	17.3	
16.0–17.9	6	18–44	33.3	
18.0–19.9	0			
20.0–21.9	2	45–56	50.5	
22.0–23.9	1	64	64	

from various streams in the Great Smokies were found to begin spawning in their third year. The spawning of wild trout at two years and at 6 inches in length is not the rule, but does occur.

An examination of the scales of more than 100 wild brook trout emphasized the difficulty of determining age by the conventional method of counting the annual growth rings. The brook trout appears to eat more freely at lower temperatures than does the rainbow, and in spring-fed streams may be fairly active all winter long except at the very coldest periods. The usual criteria of seasonal growth could not in many instances be definitely observed in the scales examined. Further study is necessary before arriving at conclusions on the growth rate of brook trout in the streams of the Great Smokies.

In the National Parks, the protection of natural aquatic communities is a definite responsibility. The taking of game fishes is an exception to the general wildlife policies, which extend protection to all organisms alike. It is felt that the minimum destruction of aquatic and bank-dwelling life results when only artificial lures are permitted. Even though the bait should be brought in from outside park boundaries, it is felt that it would not be a good conservation procedure to permit use of natural baits. The danger of introducing exotic species is minimized when minnows and other organisms cannot be used as fish bait. Considering the number of fishermen, at least 100 per mile on the more heavily fished streams, and the relatively small size of many of the streams, it is believed that better fishing is afforded by allowing only artificial lures.

The problem of size limits is a tough one that still awaits a satisfactory solution. When the number of undersized trout that must be returned to the water exceeds too greatly the number that may be retained, there is dissatisfaction on the part of the anglers, and an indication of unbalance in the fish population. To abolish the size limit would in some instances be a step forward, especially if the fishing clientele possessed a sufficiently high degree of sportsmanship to insure the safe return of small fish to the water. Unfortunately there is the tendency for the fisherman to keep any fish taken until he gets a larger one, then to discard the smallest so as to keep within the creel limit. To require that all fishes taken, regardless of size, be retained as part of the creel is unfair to the true sportsman and almost impossible to enforce. For Great Smoky Mountains National Park, the most workable solution seems to be a reasonable size limit, together with the request that all fishes above that size be retained as part of the creel. The size limits on trouts within the park are now the same as those in the States of North Carolina and Tennessee, respectively. The limit of 8 inches on rainbows is not so satisfactory as our census returns indicate. Many of the undersized trout taken are seriously injured and die. Dead or injured small trout have been seen along heavily fished streams and collected from inlets to rearing pools located on streams open to fishing. Injured fishes are good subjects for infection by *Saprolegnia* and other diseases. A study of creel census returns indicates that the size limit on rainbows over the park should be reduced to 7 inches as was done on the Tennessee side in 1940. By lowering the limit from 8 to 7 inches,

the total catch can be increased from 30 to 50 per cent. The adoption of a 7-inch limit on all species of trouts would make for simpler enforcement, and give added protection to the brook trout.

Table 7 contains findings of a census taken of Deep and Forney Creeks in 1935, and gives data of interest on the problem of legal sizes. That year the size limit on rainbows was 10 inches. 3 times as great in 1935 as in 1939. It is quite possible that many of these trout were hooked and reported more than once. It was disappointing to the angler not to be able to keep rainbows 8 to 9.9 inches in length, and a reasonable take of the fish crop was not possible. Largely on the basis of these returns the size limit on the rainbow was lowereed from 10 to 8 inches in 1936.

TABLE 7

CREEL CENSUS RETURNS FROM FORNEY CREEK AND DEEP CREEK, NORTH CAROLINA, IN 1935

Size in Inches	Species	Forney Creek	Deep Creek
Under 6	rainbow	1,080	1,240
6 to 7.9	rainbow	2,535	3,672
8 to 9.9	rainbow	3,805	4,394
10 to 11.9	rainbow	415	650
12 to 13.9	rainbow	69	106
14 to 15.9	rainbow	3	14
Total legal sized trout		487	770
Total undersized trout		7,420	9,306
Total number of anglers		650	941
Average creel		.75	.82
Miles of stream open to fishing		6	7
Av. No. legal trout per mile		81.2	110
Av. No. undersized trout per mile		1,236.6	1,329.4
Ratio of legal to undersized trout		1:15.2	1:12.1
Average size (mean) of legal trout (estimated)		10.9	10.9

This census was taken under the supervision of Maurice Sullivan, Jr., Wildlife Technician. The streams were open to fishing during June and July only. The size limit was 10 inches.

These two streams had been closed for at least two years previously and there was persistent demand from local anglers that they be opened to fishing. A two-months season, June and July, was allowed, and only artificial lures were permitted. It will be noted in comparing Tables 1 and 7 that the population of rainbows under 8 inches reported in 1939 from Forney Creek was more than double that reported in 1935. The increase in smaller fishes was probably a result of stocking fingerling trout since 1935. The number of rainbows 8 to 9.9 inches in total length was reported to be

In managing the trout streams of the Southern Appalachians, the fish manager has to choose between producing relatively few trout more than 10 inches in length for a limited group of anglers, or a larger number of smaller fish, in order to offer some recreation to an ever-increasing number of fishing enthusiasts. In nearly every case, the pressure is for more trout of legal size, and for a reasonable size limit.

REGULATIONS

The regulations affecting fishing at Great Smoky Mountains National Park

are drawn up by the National Park Service with the approval of the States of Tennessee and North Carolina. All regulations must therefore be a compromise, which aims first of all to meet the protection policies of the Service and which does not conflict with State laws. Regulations in effect during 1938 and 1939 were:

Size limit: rainbow trout 8 inches, brook trout 6 inches.

Creel limit: 10 fishes per day or in possession.

Season: May 16 to August 31.

Fishing hours: 5 A.M. to 6:30 P.M. (one hour later Eastern Standard time).

Use of natural bait prohibited, artificial lures with one hook only permitted.

In 1940, the size limits of the two States were adopted in entirety, the principal change being establishment of a single size limit of 7 inches on trout in the Tennessee portion of the Park.

SUMMARY

Many of the trout streams at Great Smoky Mountains National Park lend themselves readily to creel censuses. Such studies were conducted on 3 streams in 1938, 4 in 1939, and 5 in 1940. The catch of legal trout per mile of open water varied from 146 (Forney Creek, 1939), to 1,167 (Little River, 1940). The average catch of legal-sized trout per hour varied from .52 to 1.32, the extremes being for the same streams and years as in the preceding statement. The benefits of stocking legal-sized trout prior to and during the open season were clearly evident on Little River.

The average size (mean) of the legal trout removed did not vary significantly over the three years, except for Abrams Creek in 1940. A lowering of the size limit on rainbows from 8 to 7 inches in streams on the Tennessee side increased the catch by about 42 per cent and lowered the average size only from 8.63 (1939) to 8.33 (1940). Abrams Creek yielded trout of larger average size than did other streams in 1940 (9.82 inches). This stream has limestone water and abundant fish food. The stocking in this stream was responsible for the fish crop and was largely confined to tributary streams.

Brook trout on the whole made up only a small part of the total catch. This is because the brook trout are found in streams largely above the sections open to fishing, and adult fishes have not been extensively stocked in lower waters. Brook trout do well at the hatchery and in rearing pools at the Great Smokies, but not when stocked as fingerlings in competition with the rainbows.

An examination of the scales of 324 rainbows from 3 to 23 inches in total length indicated a wide range in growth rate, which in some instances could be attributed to environmental factors in individual streams. In most streams a majority of the wild trout of 7 to 8 inches total length are in their third summer, while in a few streams fish of the same age may be either smaller or larger. The mean weight of 30, 7 to 7.9-inch rainbows was 2.4 ounces, of 19, 8 to 8.9-inch rainbows 5.1 ounces. As a rule this species reached spawning condition in the third year.

Difficulty was found in determining the age of brook trout by the conventional method of scale analysis.

Evidence from creel census studies

and from age-length and length-weight relationships indicates that a size limit of 7 inches on rainbow trout in the Great Smokies is preferable to one of 8 inches. The restriction of lures to the artificial varieties is justified on the basis of the general faunal protection policies of the National Park Service.

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MIGRATION CENSUS OF MULE DEER IN THE WHITE RIVER REGION OF NORTHWESTERN COLORADO

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Students of game management have long known of a method to obtain estimates of game populations through track counts. Ordinarily, the application of this method depends on two things: (1) A snow or soil surface on which the tracks are readily distinguished; and (2) a movement of the game animals over the area where the count is to be made.

In western Colorado, the seasonal migration of the great White River mule deer herd provided an opportunity to apply the track count method of census. The extreme migration of the herd from summer range on the White River National Forest to the winter range on Grazing Service Colorado District No. 1 approaches eighty miles, with perhaps the average distance being fifty.

The yearlong range includes a large hourglass-shaped area between the Colorado River and the White River. During the spring and fall migrations, the deer tend to concentrate in the central, narrower portion, which is traversed by the road between the towns of Rifle and Meeker. Hence, the mass movement of the mule deer over the unpaved roadway gave ideal conditions for recording (Table 1; Figure 1) the migratory deer population.

Although the possibilities were realized for a number of years, it was not until 1938 that an attempt was made by the United States Forest Service to conduct a track count of the White River deer herd. The enumeration was incomplete, but demonstrated the practicability of the method and provided the basis for a very successful deer-track count during the spring of 1939, which is here reported upon.[1]

The count was taken each morning after obliterating the tracks of the previous day by dragging the road with pinon trees chained together and pulled by a truck. Tracks not reached by the drag were blotted out by men carrying an old broom or a piece of brush.

The road was divided into two-mile sectors that were numbered from the north; two men assigned to each. Counts were made early each morning during the migration, or from April 26 to May 31, 1939. During this period, a total of 28,207 deer tracks was recorded on the roadway. Table 1 itemizes the daily counts.

Some of the findings of the track count were:

1. Only rarely did a deer travel in the opposite direction to the general migration trend. When this occurred, the tracks were subtracted from the sector total for the day.

2. The tracks were usually individual and distinct, since a group of trailing deer would disperse at the roadway and cross without disturbing the other tracks.

3. The deer generally crossed where vegetation or land features provided some degree of shelter.

4. Generally, the deer tended to go around open and farmed areas. This ac-

[1] The Colorado Game and Fish Department cooperated in this work.

counts for Sector 7 being less used than 6 and 8.

5. The greatest number crossed during the early morning.

6. It was found that the deer did not stop after crossing the road, but moved on several miles toward their summer range.

7. The does and yearlings started to migrate before the bucks.

8. It was observed that a drop in temperature, especially if accompanied by stormy weather, resulted in a slowing down of the migration; note counts for April 30, and May 12, 13, 16, and 17.

9. The migration first reached full volume at the lower elevations and gradually progressed to the higher areas. This explains the shift in the count from the lower numbered sections to the larger ones as the census period advanced.

10. The migration got under way slowly, then increased rapidly to a peak, after which it decreased sharply, as indicated by the graph.

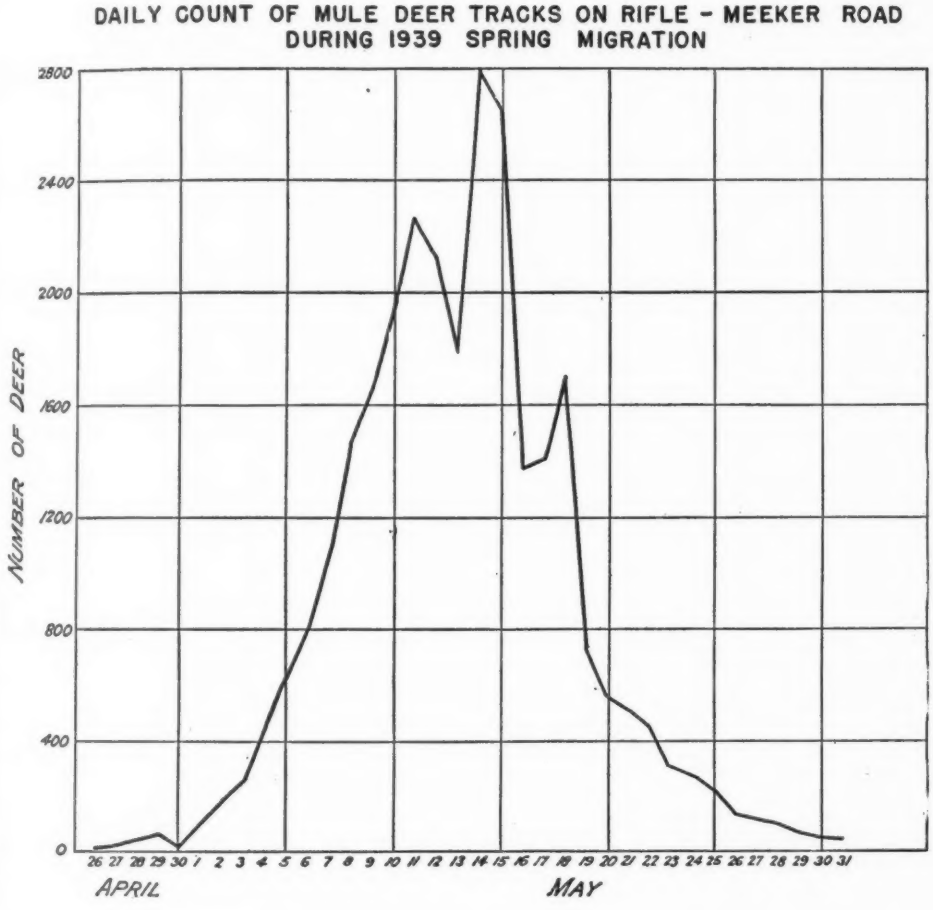

TABLE 1

TABULATION OF TRACKS BY DAY AND SECTOR TO SHOW TOTAL NUMBER OF DEER CROSSING RIFLE-MEEKER ROAD DURING 1939 SPRING MIGRATION

Date	Sector Number											Daily Total
	1	2	3	4	5	6	7	8	9	10	11	
April 26			3	2								5
27												#27
28			15	33							1	49
29		7	17	25	2					5	1	57
30					3	2	2					7
May 1												
2	2	50	34	27	19	7		15		10	2	166
3	30	23	56	57	17	8	2	15	17	6	7	238
4	30	†116	75	115	34	12		22	14	4	21	443
5	†30	†83	†110	176	44	46	11	65	38	3	24	630
6	46	79	127	185	50	30	†24	128	75	3	44	791
7	3	99	140	359	54	96	3	137	145	4	31	1,071
8		120	262	343	162	73	29	219	159	8	87	1,462
9	57	108	151	286	153	143	66	292	230	41	127	1,654
10	81	75	174	183	335	203	80	340	220	74	181	1,946
11	37	135	198	452	244	197	82	397	276	71	176	2,265
12	54	95	230	308	186	214	137	332	384	81	105	2,126
13	20	46	114	222	112	173	†117	380	325	97	187	1,793
14	60	80	205	250	195	118	101	617	760	170	240	2,796
15	64	76	92	288	186	147	71	630	595	176	323	2,648
16	6	28	33	103	46	68	28	495	350	113	99	1,369
17	21	20	36	129	40	83	31	430	325	137	161	1,413
18	12	17	19	32	103	54	34	678	515	113	138	1,715
19	3	6	24	48	38	52	28	152	165	76	121	713
20	5	15	23	82	86	11	9	91	93	60	78	553
21	5	15	7	53	68	21	5	79	102	73	87	515
22	8	6	16	52	31	17	7	80	87	68	76	448
23	3	6	16	22	17	19	2	31	85	46	49	296
24	2	1	3	32	24	19	4	37	96	25	29	272
25				16	11	11	9	45	69	25	37	223
26				11	11	10		5	12	25	57	131
27				1	2	10		27	16	36	26	118
28						5		21	22	21	31	100
29						6		12	17	2	35	72
30								9	14	17	10	50
31								13	8	8	16	45
Totals	579	1,301	2,180	3,892	2,277	1,856	882	5,794	5,241	1,598	2,607	28,207

† Check lost because of sheep; figure used is average of adjoining sectors.
# Figure used is average of preceding and following days.

A much more accurate count was obtained by this method than by any other that had heretofore been tried in the area. It is believed this census method is particularly worthy of consideration in regions whose physical features and migration characteristics are similar to those in the White River territory.

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ON THE ANALYSIS OF PRODUCTIVITY IN POPULATIONS OF HIGHER VERTEBRATES[1]

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The natural productivity of mammals and birds, especially of game species, has received a great deal of investigative attention during the past decade. Valuable information has resulted from this work, but investigators, by assuming (or by leaving the reader to infer) that the loss of a clutch of eggs or a litter of young *necessarily* means that much net loss in productivity, may introduce errors of such magnitude that critics could, in many instances, appropriately ask whether the conclusions were not as misleading as instructive.

It may be conceded that various species for reasons of latitude, climate, rarity, inherent shortness and lack of synchrony of sex rhythm (Allen, 1934) physiology, psychology, etc., may have distinctly limited opportunities to reproduce. Late young—even of species that readily renest throughout a long breeding season—may be, moreover, few in number, subject to pronounced if not lethal handicaps, or undesirable from special human viewpoints.

Nevertheless, calculations of so-called life equations that ignore, for example, renesting when its compensatory value is substantial can lead pretty wide of the truth; and the "common sense" reasoning of administrators and sportsmen to the effect that every game bird egg that fails to hatch is the equivalent of one less hunting season pheasant (or quail or duck or something else) should hardly be surprising as long as comparable assumptions continue to be made by those whose studies are accepted as technical background. We have only to consider standard practices in poultry management to see how immense numbers of eggs would never be laid in the first place were it not for the stimulus resulting from removal of eggs from laying hens. Among wild-living birds, the flicker (*Colaptes auratus*) has long been known for its propensity for continuing to lay after egg losses (Bent, 1939: 272). Recognition of some of the "fallacies of misplaced concreteness" (Whitehead, 1925; Henderson, 1941) that are so prevalent in life history analyses should be possible without unduly minimizing loss types of real importance.

My own endeavors to evaluate renestings and related phenomena were inspired by Stoddard's (1931) classic investigation of the bobwhite (*Colinus virginianus*) in Georgia and Florida, which clearly distinguishes between percentage and significance of nesting losses. On pages 224 and 225 of his book, we may not only read that "from 60 to 80 per cent of unsuccessful nesting attempts may normally be expected at large over the Southeastern quail territory" but also that, in the course of a season, "the majority of the pairs sooner or later are successful in hatching

[1] Journal Paper No. J-674 of the Iowa Agricultural Experiment Station, Ames, Iowa, Project No. 498. Fish and Wildlife Service (U. S. Department of the Interior), Iowa State College, Iowa State Conservation Commission, and the American Wildlife Institute cooperating.

off a brood." In a Wisconsin study, over 80% of the hens may, on fair evidence, be judged to have produced young, despite a loss of 51% of the nests (Errington, 1933). Later, a study of the ring-necked pheasant (*Phasianus colchicus torquatus*) in northwestern Iowa demonstrated some degree of success for only 23.1% of 445 nests under regular observation (Hamerstrom, 1936), but analysis of the data suggested that from 70% to 80% of the hens hatched out the one brood per season that typically satisfies them (Errington and Hamerstrom, 1937).

How widespread such compensatory reproduction may be is imperfectly indicated by current literature. The Hungarian partridge (*Perdix perdix*) has some renesting ability (Yeatter, 1934: 81; Middleton, 1936: 804; Errington and Hamerstrom, 1938). Prairie chickens (*Tympanuchus cupido americanus*) probably re-nest although to a lesser extent than bobwhites, Hungarian partridges, and pheasants (Hamerstrom, 1939: 115); and this statement may be applicable to other grouse (Tetraonidae). One would not expect waterfowl to do much if any renesting during the short summer of the Arctic regions, but, farther south, where the active breeding season extends over a period of months, renesting by Anatidae, Rallidae, and perhaps other groups surely offsets some of the early failures.

It has long been known that many passerine birds respond to nest failures by laying another clutch of eggs, usually some days after the failure. This is mentioned in recent monographic writings by Miller (1931) for shrikes (*Lanius* spp.), Nice (1937) for the song sparrow (*Melospiza melodia*), Kendeigh and Baldwin (1937) for the house wren (*Troglodytes aedon*), Hann (1937) for the oven-bird (*Seiurus aurocapillus*), Erickson (1938) for the wren-tit (*Chamaea fasciata*), Wallace (1939) for Bicknell's thrust (*Hylocichla minima bicknelli*), and Blanchard (1941) for the white-crowned sparrow (*Zonotrichia leucophrys*).

Of the wren-tit, Erickson (1938: 282) writes that "Pairs which successfully fledged young have been watched, but no evidence of repetition of nesting cycle, once it is completed, has been found" and she has "records of as many as four and five attempts to raise young on the part of one pair, and of the initiation of a new cycle when the brood was lost when about ten days old." For multiple-brooded species, the difficulty of distinguishing between failure-induced layings and the normal complement of clutches naturally complicates analyses; and, after studying Nice's (1937) voluminous data on the song sparrow and Emlen's (1941) experimental analysis of the breeding cycle in the tricolored red-wing (*Agelaius tricolor*), I must confess to a doubt that the complexities of the breeding equation in such forms would permit an accurate measurement of compensatory reproduction.

Among mammals, the equivalents of these compensating phenomena are doubtless less pronounced, yet they could very possibly be of frequent occurrence in species that characteristically give birth to litters at short intervals during a long breeding season. The muskrat (*Ondatra zibethicus*) is the only species in the latter category with which I am intimately familiar, and the findings from eight years of work on population recovery in Iowa (largely unpublished) suggest that poor success early

in the breeding season is a major stimulus to exceptionally long-continued breeding. One of the clearest examples came out of the work at Round Lake, near Ruthven, Iowa, in 1935, a year of notable overpopulation. On roughly one-half of the marsh, losses from causes other than intraspecific strife were not great, but breeding stopped by mid-summer, apparently in consequence of population tensions. On the other half, losses through predation and disease predominated, intraspecific antagonism was far less intense, and nearly all of the late summer litters—usually the third and fourth of the season for individual females (Errington, 1937b and unpublished)—were born on sections of the marsh where known early-summer mortality of young had been highest.

I have been unable to find reference to compensatory reproduction (under that or any other name) in the literature devoted to mice of the genera *Microtus* and *Peromyscus*, but some of the data would seem to suggest the operation of such a mechanism. One may ask, for instance, how much Bailey's (1924: 528) record of 17 consecutive litters born within a year to a captive *Microtus pennsylvanicus* was conditioned by human removal of young from the cage.

On the whole, if an investigator wonders that the bird or mammal he is studying can exist at all in the face of the losses of eggs or young that take place—and the species not only exists but maintains abundance, often in spite of drastic annual losses of adults—he may well try to inquire into the matter of possible compensations.

This paper is prepared in the hope that it may be helpful to workers who are conscientiously striving to make their calculations of productivity as nearly accurate as they can. Suggestions are intended for broad, rather than highly specific, guidance, for each species patently has problems that are more or less peculiar to itself and which, furthermore, vary with locality and season. The procedures outlined have their crudities and their limitations of scope, and I do not claim more for them than that they are the product of direct and indirect experience with several life history investigations of higher vertebrates.

GROUNDWORK FOR AN ANALYSIS OF COMPENSATORY REPRODUCTION

"Renesting" of birds is a term that applies to reproductive efforts resulting primarily from previous failures. In view of the technical obstacles to tracing renestings in multiple-brood small birds and the equivalent in multiple-litter mammals, this exposition will treat with the simpler sort of problem that an investigator can reasonably hope to work out.

Let us then consider, as representative of a number of familiar species, a hypothetical bird that is satisfied with the hatching of one brood a year and that renests after ordinary failures at least during the early part of an April to July general nesting season. We may remain in touch with actuality by following the trends of Hamerstrom's (1936) data on the ringnecked pheasant, with sufficient changes made in numerical values to aid the reader in keeping track of the sources of the figures in the simple algebraic equations to follow.

Table 1 presents the kinds of data that can be obtained for almost any

avian species through employment of usual techniques (Errington, 1932). Although the breeding season for our hypothetical species is divided into half-month periods, an investigator whose data are exceptionally complete might find shorter divisions advantageous. Establishing the date of beginning just after the laying of the last egg of a complete clutch), and about 20 days for the laying of the clutch (our species lays an egg a day on most but not all days of this period), we get a time interval of about 46 days and trace the laying of the first egg to the second half of April.

TABLE 1

HYPOTHETICAL SAMPLES OF CORRECTED[1] DATA ON SUCCESS AND FAILURE OF CLUTCHES FOR WHICH TIME OF LAYING OF FIRST EGG IS KNOWN

Periods in which clutches were begun	*Number of clutches*	*Successful*[2] *clutches*	*Failed clutches*
Periods of initial nesting attempts:			
First half of April	19	2	17
Second half of April	35	12	23
First half of May	52	22	30
Second half of May	54	26	28
Periods following initial nesting attempts:			
First half of June	45	21	24
Second half of June	20	10	10
First half of July	8	3	5
Second half of July	1	0	1

[1] Correction for analytical purposes made by excluding from the table clutches barely begun before failure and the failure of which obviously had little or no significance from the standpoint of productivity. In practice, these excluded clutches are mainly single abandoned eggs, either in nests or "dropped" at random.

[2] A clutch is listed as successful if any young are hatched from it.

ginning of clutches is largely done by calculating backward from facts known about each clutch, the rate of egg-laying and the length of the incubation period for the species. Undetected losses of individual eggs are an occasional source of error—usually insufficient to result in assignment of a clutch to the wrong half-month period.

Hypothetical examples of dating:

Clutch "A," 18 eggs, was known to have hatched a few days before the last observation on June 10. Allowing 3 days for time between dates of hatching and the visit at which the fact of hatching was noted, 23 days for incubation (which for our hypothetical species be-

Clutch "B," 17 eggs, was destroyed by mowing on July 20, shortly before hatching. Although we may not be able to determine the exact date of laying the first egg, we can surely place it in the first half of June.

Clutch "C," 21 eggs, was destroyed by predators about May 30, after having previously lost 2 eggs through unknown cause. Four eggs recovered for examination contained embryos of about 10 days' development. Allowing 26 days for laying of the clutch and 10 for incubation, we assign the beginning to the second half of April.

Clutch "D," 10 eggs, was laid in the same nest as Clutch "E," 19 eggs; from

the end of a temporarily double rate of egg deposition (2 eggs a day for 3 consecutive days), the nest was judged to have been deserted by hen "E" soon after hen "D" apparently began laying (about May 24) and deserted in turn by hen "D" about June 4. All eggs were unincubated when examined June 9, after it had been made sure that hens were no longer using the nest, so the time of laying of first egg for clutch "E" was determined as the first half of May.

Clutch "F," 3 eggs, was abandoned after disturbance, May 7, long before completed. It obviously was begun early in the first half of May.

Clutch "G," 2 eggs laid "parasitically" in the nest of another species[2] between June 4 and 8, was considered in the same category as a "dropped" egg or a single-egg abandoned clutch, hence omitted from analytical calculations (see first footnote to Table 1) even though date of laying could be assigned to a half-month period. Parenthetically, it may be explained that this sort of "parasitism" typically has no reproductive value, in contrast with the "parasitism" of the cowbird (*Molothrus ater*) (Friedmann, 1929; Nice, 1937: 152–165).

The fundamental question of what proportion of clutches constitute renesting attempts is not one to which reliable answers may always be forthcoming. Bennett (1938: 57–59), in his monograph on the blue-winged teal (*Querquedula discors*), designated as renestings the late, poorly-constructed nests concerning which there could be little doubt, but, as I see it, these may strictly be considered only as *late* renestings. Incomplete or unincubated clutches broken up or abandoned early in the nesting season are surely followed in a large number of instances by renestings that cannot on basis of dating or appearance be distinguished from initial attempts; and, in these instances a renesting often stands as good chance to produce a full-sized, early-season brood as many clutches that were actually the first laid by individual females. Indeed, if an investigator is working with a species, the hens of which are habitually careless about where they lay their first few eggs, and gives "dropped" eggs and freely deserted single-egg nests the status of lost clutches in his notes, he may well consider whether most of his "regular" nests should not be counted as renestings.

Calculations of possible time of renesting of hens after failures are beset by two analytical hazards in particular. One relates to the proportion of nest failures due to mortality or incapacitation of the hen, and the investigator who finds this factor to be either immaterial or easily measurable is fortunate. Let us say that, for our hypothetical species, the losses of 11 of the clutches begun up to the middle of July and dated as in Table 2 were known to have followed or accompanied losses of the hens.

The second hazard arises from uncer-

[2] Such "parasitism" was frequently observed among ground-nesting game birds of northwestern Iowa (Hamerstrom, 1936: 180; Bennett, 1936; Errington and Hamerstrom, 1938). Low (1941: 510–511), studying mutual "parasitism" by redhead (*Nyroca americana*) and ruddy (*Erismatura jamaicensis rubida*) ducks, found that "the amount of promiscuous egg laying was directly proportional to the amount of unsuccessful nesting during each season of study."

tainties in judging when to expect a hen to resume laying after a failure. In many common species, if failure occurs early or in mid-season before the clutch is complete, renesting may follow much as a continuation of the failed effort, though perhaps with some "egg-dropping." When failure occurs during incubation, the probable time of renesting and, following Riddle (1911: 482), we read that the "time interval between the beginning of rapid growth of the 6 mm. egg, and the breaking of the egg from the ovarian follicle (ovulation) is normally between five and eight days." We also learn from the experiences of poultrymen that prolonged incubation of a failed clutch may deplete a bird's

TABLE 2
HYPOTHETICAL SAMPLES OF CALCULATIONS ON POSSIBLE TIME OF RENESTING OF HENS AFTER FAILURES[1]

Periods in which failed clutches were begun	Number of clutches failing	Number of failures positively terminating breeding efforts, as through death of hens	Number of failed clutches for which renesting attempts may be expected in specific half-month periods						
			Periods of initial nesting attempts			Periods following initial nesting attempts			
			Second half of April	First half of May	Second half of May	First half of June	Second half of June	First half of July	Second half of July
Periods of initial nesting attempts:									
First half of April	17 of 19		1	7	6	2			
Second half of April	23 of 35			11	5	4			
First half of May	30 of 52	1			13	9	3	4	
Second half of May	28 of 54	5				15	3	4	1
Periods following initial nesting attempts:									
First half of June	24 of 45	2					12	4	3
Second half of June	10 of 20	1						3	2
First half of July	5 of 8	2							1

[1] See text for explanation of methods.

should be calculated with reference to records from artificial propagation, all available sources of information including the literature, experimentation with captives, and observations of marked individuals living in the wild.

To avoid making our hypothetical problem too complex, let us say that reproduction in our species is in many ways comparable to that of the domestic fowl. It has either a long sex rhythm or one that recurs so frequently as to be virtually continuous for the duration of the laying season. The most rapid resorption of ova after cessation of laying may be expected, as for the fowl (Stieve, 1918), in the first 5 days; physical reserve to the point that she may require a rest before renewing her reproductive efforts—in a closely related wild bird possibly a week or two, judging from the rapidity with which pheasants recover weight lost from hunger (Errington, 1939a: 35).

Table 2 shows the renesting periods assigned to hens after failures, as estimated from the status of clutches at time of failure and from careful guesses as to physical condition of hens that lost clutches during incubation. Previous elimination from the tabular data of single-egg, and some other very small, lost clutches (first footnote, Table 1) reduces the error due to certain

hens losing one clutch and starting another in the same half-month period; at any rate, it should be less hazardous to assume, for convenience of analysis, that renesting doesn't occur within a short period than that it doesn't occur within the nesting season. The use of shorter than half-month periods would reduce possible errors from this source still further, provided that data were available concerning sufficient nests (several hundred or more) to permit subdividing without getting down to samples too small to be representative. Ample, good-quality, field data on broods are about the best safeguard against gross imperfections in appraisals of renesting activities.

Taking the hypothetical examples of clutches "A" to "G," we may attempt to predict periods of renesting:

Clutch "A," through success, terminated the season's breeding for the hen.[3]

Clutch "B," destroyed near its hatching point on July 20, was begun in the first half of June; but, considering the lateness of the season and the breeding status of the hen at the time of failure, it is unlikely that renesting followed.

The loss of clutch "C," begun in the second half of April and destroyed after about 10 days of incubation about May 30, was probably followed by a delayed nesting. After 10 days of incubation, the hen's ova would be pretty well resorbed, and the bird would require something like a week or perhaps longer to resume laying; irrespective of uncertainties as to the exact date of renesting, the time could reasonably be set as within the first half of June.

Renesting almost certainly followed the abandonment of clutches "D" and "E," within the first half of June and the second half of May, respectively.

The hen deserting the small, very incomplete clutch "F" on May 7 may be expected to continue her laying scarcely without interruption and, even if she "dropped" an egg or two about the countryside, to have another clutch started in the second week of May. In calculations using half-month periods, clutch "F," being followed by renesting in the period of its origin, would be ignored, though it could be handled in calculations having a weekly basis. On the other hand, clutches in the class of "G" (including the "dropped" and the single abandoned eggs in nests) could best be treated as if they had never existed, unless the tabulation periods could be shortened much more than now looks feasible.[4]

Completeness of clutches is hard to recognize before incubation, and even then error may have been introduced by undetected disappearances of eggs and contributions to a clutch by more than one hen. This granted, we may still find computations of the average number of eggs in complete clutches according to half-month (or other length) periods useful, not only for what help they may later be in dating the origin of broods but also because of the clues often afforded for comparison with other

[3] The reader should not be misled by the fact that typically one-brood-per-season species may have second broods as a result of manipulation (Bissonnette and Csech, 1941) or because of other special circumstances.

[4] In practice, a limit to the shortening of the tabulation periods for the nesting data may be imposed by the relatively greater difficulty of assigning brood data—which are highly important for purposes of correlations—to short periods.

species. The number of successful nests yielding data on number of young hatched is likely to be less than the number of nests known to be successful,

Let us now say that our hypothetical species can be studied during the post-nesting months and that data on broods proved valuable in the guidance and

TABLE 3
HYPOTHETICAL SAMPLES OF DATA ON SIZE OF COMPLETE CLUTCHES AND NUMBER OF YOUNG HATCHED PER SUCCESSFUL CLUTCH

Periods in which clutches were begun	*Number of complete clutches*	*Average number of eggs laid per complete clutch*	*Number of successful clutches*	*Average number of young hatched per successful clutch*
Periods of initial nesting attempts:				
First half of April	9	19.4	2	13.0
Second half of April	9	13.7	10	10.6
First half of May	32	13.3	21	10.0
Second half of May	28	10.6	25	9.1
Periods following initial nesting attempts:				
First half of June	23	9.2	19	8.0
Second half of June	16	9.0	10	7.7
First half of July	7	7.9	3	6.5
Second half of July	1	7.0	0	

for sometimes so many of the shells of hatched clutches become scattered or destroyed that an investigator has all he can do to make sure of the fact of hatching; and, in addition to the losses of individual eggs, there are the young that die soon after hatching and are for various reasons undiscovered at the time the nesting site is examined.

The seasonal decrease in size of hypothetical clutches and in number of young hatched is more uniform in Table 3 than would always be found in actuality; otherwise, the tabulations follow the pattern of the northwestern Iowa pheasant data. Considerable individual variation in size of completed clutches and of newly hatched broods may also be expected throughout the nesting season, so it doesn't follow that a clutch has to be early if large, or late if small.

verification of calculations having to do with the nesting, as well as serving as indicators of early juvenile mortality. Table 4 summarizes certain data obtained up to about the middle of August, after which identity as specific

TABLE 4
HYPOTHETICAL SAMPLES OF BROODS OBSERVED IN THE FIELD AND CALCULATED TIME OF BEGINNING OF THE CLUTCHES FROM WHICH THEY WERE HATCHED

Periods in which clutches were begun	*Broods observed*
Periods of initial nesting attempts:	
First half of April	8
Second half of April	65
First half of May	110
Second half of May	80
Periods following initial nesting attempts:	
First half of June	20
Second half of June	5
First half of July	2

broods tended to become obscured through separation and interchange of members.

Ages of broods observed in the field were estimated from the size of the young. The approximate dates of laying of the first eggs in clutches from which the broods hatched were computed from the hatching dates with the assistance of the data given for each half-month period of Table 3.

For an example, we may trace a brood of 8 young of an estimated age of 7 weeks on August 10. These young would have hatched from a clutch for which incubation would have begun about the last of May. From Table 3, we may see that the average number of eggs in complete clutches begun in the first half of May was 13.3 and that the average number of young hatching was 10; for the second half of May, the averages were 10.6 eggs and 9.1 young. Refinement of calculations would be spurious because of variables—especially since the beginning date for the clutch would fall close to the middle of the month—but assignment to the first half of May would seem most in keeping with probabilities.

Obtaining requisite quantitative data on the young that a species has to show for a breeding season may be as important as anything an investigator can do in a study of productivity, yet data of this type are not presented in the literature to the extent that one might think they could be. They are often among the most difficult data to amass, however, particularly for species having secretive young that live in habitats where visibility is poor. To my inability to obtain more data on broods in dense summer vegetation may be ascribed some of the main shortcomings of my early attempts to analyze productivity of bobwhites in southern Wisconsin (Errington, 1933). The faculty that muskrats have for staying out of sight between their weaning and "kit" stages (Errington, 1939c: 472–474) would not be such a handicap to detailed correlation of breeding data and population recovery in Iowa if a method could be discovered for closely determining ages of the general run of subadults taken by trappers; growth and developmental rates have been shown by tagging and other data to be so variable (Errington, 1939c; 1941a: 85–86) that the prospects of determining ages of unmarked winter specimens to within a half-month, or a month, of their actual time of birth seem discouraging.

Derivation of a Procedure for Calculating Periods at Which a Reproductive Stage Begins

This section could logically relate to groups other than single-brood birds, but its scope will be restricted to our hypothetical species and only to periods at which the hens begin to lay.

While the reproductive activities of a limited number of individuals may under favorable conditions be studied to excellent advantage through marking for field recognition (Nice, 1937; Edminster, 1938a; Emlen, 1939; 1940; Wright, 1939; Trippensee, 1941), the algebraic treatment of mass field data may hold even greater promise for some types of studies intended primarily to give a general picture.

The basic procedure that seems most adapted for use with our hypothetical species is to handle the data for *each* of the half-month periods by means of the

formula: number of hens laying multiplied by fraction of clutches succeeding equals number of broods. The number of hens laying is synonymous with the number laying for the first time only during the early part of the laying season; thereafter, values for the number of hens beginning to lay in a given period must be indirectly derived. It is to be emphasized that calculations as to periods of first-laying for the season must be governed by the data given in Tables 1, 2, and 4.

The fewness of observed broods hatching from clutches begun either before the middle of April or after the middle of June defines the span of the season for effective laying, and, of the broods observed, by far the greater number were produced from clutches begun before the first of June (Table 4). As the laying season is distinctly on the wane by June, there should be scant risk in assuming that few if any of the hens lay their first eggs later than the second half of May—an assumption which we may say is borne out by gonadal studies of hens collected at random for specimens or carcasses of victims of accident and predation. Let us also say that the proportion of non-breeding hens shown by the specimen postmortems was negligible.

Before setting up and solving the equations, let us designate the number of hens beginning to lay in the first half of April as "a"; the number beginning to lay in the second half of April as "b"; in the first half of May, "c"; and in the second half of May, "d." Hens "a," "b," "c," and "d" comprise the total number of breeding hens of which the combined efforts (first nestings plus renestings) are necessary to produce the total number of broods hatched from clutches begun in April and May. The number of hens and the number of broods should be regarded as samples—each as valid in relation to the other as is consistent with the tabulated data—not as absolute densities unless the investigator actually does know the total number of hens and broods living on a unit of land.

From Table 1, we see that 2 of 19 clutches begun in the first half of April were successful and, from Table 4, that 8 broods were credited to clutches so begun. The number of hens laying is near enough to the number beginning to lay in the period, or "a," so we may set up the equation, $\frac{2a}{19}=8$, with expectation only of the minimal inaccuracies inherent in the data as subdivided into half-month periods. The value of "a" is then 76 hens.

The number of breeding hens for the second half of April includes both those laying for the first time in the period ("b") and the "a" hens now renesting. The fraction of the "a" hens renesting in the second half of April is $\frac{1}{19}$ according to Table 2, or $\frac{7}{19}$ or 4 hens. The 4 hens plus "b," multiplied by the fraction of success for the period ($\frac{12}{35}$, as in Table 1) equals the number of broods (65, Table 4), and we have the equation $\frac{12}{35}(b+\frac{a}{19})=65$. Substituting the known value for "a," we have $\frac{12}{35}(b+4)=65$, in which the value of "b" proves to be 186 hens.

In the next equation, we have, in addition to the hens laying their first eggs in the first half of May, the "a" and "b" hens that are renesting in the period. In Table 2, the fraction of first half of April clutches followed by renestings in the first half of May is $\frac{7}{19}$ and the

number of "a" hens thus renesting is $\frac{7^a}{19}$; we also see that $\frac{1}{35}$ of the second half of April clutches are followed by renestings and that the number of "b" hens renesting is $\frac{1}{35}^b$. The fraction of nests succeeding for the period is $\frac{22}{52}$ (Table 1) and the number of broods is 110 (Table 4). In the equation, $\frac{22}{52}(c+\frac{1}{35}^b+\frac{7^a}{19})=110$, we may substitute the known values for "a" and "b" and get $\frac{22}{52}(c+58.5+28)=110$, or a value of 174 hens for "c."

For the second half of May, the nesting effort consists of all period renestings and the initial laying of the "d" hens. By applying the data given for the period in Tables 1, 2, and 4 and following the procedure outlined, we may set up the equation, $\frac{22}{54}(d+\frac{13}{52}^c+\frac{5}{35}^b+\frac{6^a}{19})=80$, which, after substitution of known values, gives us $\frac{22}{54}(d+43.5+26.6+24)=80$, or 72 hens as the value for "d."

Our calculations therefore show that a population of about 508 hens—with the fortunes indicated by the tabular samples—would be required to produce the 263 broods credited to April and May; 51.8% of the hens have thus far succeeded, and some success for clutches begun after May is shown by data on later broods (Table 4).

As the breeding season runs into June, inaccuracies in data and calculations may be expected apart from those resulting from diverse origin of data and the statistical weaknesses of the smaller samples. The Table 4 data, because of difficulties in seeing newly hatched birds during the last days that general brood counts retain any reliability, are suspected of showing a lower than actual proportion of late broods; but the greatest doubts pertain to the renesting schedule of Table 2 for June and July.

Balancing the data of Tables 1 and 2 against the corresponding brood data of Table 4 for the first half of June, we may set up a test equation, $\frac{21}{45}(\frac{15}{54}^d+\frac{9^c}{52}+\frac{4}{35}^b+\frac{2^a}{19})=20$, in which we do not have to solve for any new values but have only to substitute available figures for the hens. Since 1,667.4 does not equal 900, the nesting data and renesting calculations are not even in approximate agreement with the brood data, and we may feel that our suspicions are founded.

The above discrepancy may of course cast some question upon the accuracy of the April–May equations, in which event about all that can be said is that the calculations for these months followed fact-guided sequences and that the collective error should be much less before the breeding slackens and during times when fewer technical obstacles are imposed by field conditions and behavior of the birds.

Calculation of Productivity for a Breeding Season

Continuing with our hypothetical species but using 100 hens as a sample, we may attempt a calculation of nesting productivity on a percentage basis.

In the first half of April, 76 or 15% of the 508 "a," "b," "c," and "d" hens, or 15 of the 100-hen sample, are judged to be laying for the first time. From Table 1, we may see that $\frac{2}{19}$ of the clutches begun in the period are successful, so from the 15 hens we get 1.6 successful clutches and 1.6 hens retiring for the season from further breeding because of their success. This would leave 13.4 unsuccessful "a" hens, of which,

according to Table 2, $\frac{1}{17}$ or 0.8 are scheduled to renest in the second half of April; $\frac{7}{17}$ or 5.5 in the first half of May; $\frac{6}{17}$ or 4.7 in the second half of May; and $\frac{2}{17}$ or 1.6 in the first half of June. Table 3 shows that an average of 13 young or a total of 21 hatched from the 1.6 successful clutches begun in the period.

In the second half of April, we find that 185 or 36.4% of the "a," "b," "c," and "d" hens, or 36.4 of the 100-hen sample, are laying for the first time, and that by adding to the 36.4 the 0.8 due to renest in this period, we get a laying population of 37.2 hens, of which the current efforts of $\frac{12}{35}$ are successful.

Procedures for using the tabulated data should by now be sufficiently clear as to make unnecessary further step-by-step exposition.[5]

No data show success for clutches begun in the second half of July, so the possible nesting attempts indicated for this period in Table 2 may be ignored. Possibly only a few of the renestings scheduled for the first half of July and even the second half of June are valid. Be that as it may, since fewer than 9% of the hens by the most generous of calculations begin successful clutches after the middle of June, our figures for the entire nesting season should not be thrown off very far by any likely errors; and we may calculate that about 70 of the 100 hens were successful and hatched out in the vicinity of 650 young, or averages of 6.5 young per original hen and over 9 per successful hen. Over 8 of the original 100 hens were listed as lost during the nesting season, which would probably leave a post-nesting population of about 90 hens and about 20 hens unsuccessful but alive.

The calculations that between 70% and 80% of the pheasant hens studied in northwestern Iowa produced young were verified by hen:brood ratios obtained in late July and early August. "During this period of approximately two weeks, between the virtual termination of the nesting season and the main moulting season . . . 106 hen pheasants and 83 broods totalling 441 young were seen. . . . The average size of the broods was 5.31 young at an average age of a little less than 6 weeks, or an average of 4.16 young for all hens seen at this time of the season" (Errington and Hamerstrom, 1937: 13). The same authors (page 16) showed an average decline in size of broods from 8.7 young at hatching to 5.26 at six to seven weeks.

It should not be necessary to list hen:brood ratios or data on seasonal shrinkages in size of broods for our hypothetical species to emphasize the fact that without such data neither confirmation nor disproof of the nesting season calculations may be very convincing.

As indicated earlier in this writing, brood data, in addition to being valuable for checking against nesting data, may also be some of the best indices of juvenile mortality at times when this factor may otherwise be difficult if not

[5] Readers may also consult Errington and Hamerstrom (1937) if they wish to see application to a bona fide problem, especially pages 10 and 11 (Table 5). As two confusing errors were missed in proof-reading the paper for the original publication, "52" should be substituted for "42" in the last equation on page 8 and "Table 4" for "Table 6" in the first line of the second column on page 12.

impossible to measure or even to detect qualitatively. All work on broods should be guided and appraised with reference to social habits of the species, reactions to observers, and the many other pertinent variables.

Another index of seasonal productivity that may be useful is the ratio of adults to grown young shown by the general population at nonbreeding periods of the year. Except when migration or segregation is differential, or sampling methods are selective rather than random, many investigators may profitably inspect the bags of hunters (or the catches of trappers, when furbearers are the objects of study) to procure sex and age ratios. With some species, as the quails, the season's grown young may be sorted from older specimens on the basis of external characters (Stoddard, 1931: 75; Sumner, 1935: 225–226; Starker Leopold, 1939); with others, postmortem inspection of gonads is necessary.

Finally, if the species worked with is, like the northern bob-white, essentially sedentary, localized in ecological "islands," and easily counted in winter, comparison of population densities from the end of one winter to the beginning of the next may be a good measure of recovery from breeding stock. The method must be used with discretion, however, for pronounced variables may have to be considered even for the same areas (Errington and Hamerstrom, 1936: 312–333; Errington, 1939b; 1941b).

Let us now suppose that we have managed to work out in a satisfactory manner the productivity of our hypothetical species for a year or, better, for a term of years. We have pieced together a "life-equation" in which we can account for gains and losses, item by item. Yet, this balance sheet alone tells only part of what we need to know for an understanding of productivity. We should not overlook differences associated with geography, climate, human practices in land use, availability and juxtaposition of food and cover, and the presence of specific diseases and enemies; but, aside from these, there may be population phenomena of sufficient importance that their neglect in an analysis may nullify many of the broader conclusions arrived at. On the principal areas where recovery data on bobwhite populations are available in north-central states, the rate of annual increase has tended to be in inverse ratio to the breeding densities, almost irrespective of the variables of weather, agriculture, and predation (Errington and Hamerstrom, 1936: 421–423; 1937: 17; Errington, 1937c; 1941b; Aldo Leopold and Errington, MS);[6] and analytical dissertations on good or bad breeding seasons fall very short of their potentialities if made without reference to density factors when these are the most influential of all. On the other hand, in southeastern United States, the bobwhite appears to be much more sensitive to local influences other than density factors (Stoddard, 1931; Komarek, 1937; Errington and Stoddard, 1938; Stoddard and Komarek, 1941).

An investigator should consider as

[6] Recovery rates of bobwhite populations may, however, show atypical depression as an apparent result of space-competition with pheasants and some other wild gallinaceous birds or at the "trough" of periodic cycles of other species (Errington, 1941b: 94–100; Aldo Leopold and Errington, MS).

well as he can the possibility of many types of losses being intercompensatory in their net significance—losses that remain about the same in their aggregate despite changes in intensity of depredations by specific enemies and other local and seasonal variables (Errington, Hamerstrom, and Hamerstrom, 1940). Sometimes this intercompensation appears to be a function of population density *per se* (McAtee, 1932); sometimes of population density in relation to the capacity for accommodation of a habitat (Errington, 1937c; Errington, Hamerstrom, and Hamerstrom, 1940). Sometimes, the intercompensation looks very nearly complete; sometimes, partial; sometimes, inconsequential; furthermore, it may sometimes be spectacular at one season of the year, and unrecognizable at another.

Edminster (1939) found that predator control reduced nesting losses of the ruffed grouse (*Bonasa umbellus*) on New York experimental areas but that little or no reduction of brood losses was accomplished either by "complete" or selective control. King (1937: 525) states that juvenile mortality of the ruffed grouse in Minnesota " . . . is normally at least 75 per cent, some years even larger," but that " . . . the several hundred nests for which we have records show nest destruction from all causes to be slightly less than three per cent." During the strongly upgrade and peak years of the periodic grouse cycle, the data from good range presented by King (1937: 529) and Edminster (1938b: 826–828[7]), as well as Errington's (1937a) figures for very low ruffed grouse densities in marginal environment, show broadly inverse rates of increase from breeding stock similar to those noted for northern bobwhite populations (Aldo Leopold and Errington, MS).

Furniss (1938: 24) reports practically the same percentage of Saskatchewan duck nests hatched in each of two years, although the percentages of nests lost from different causes varied materially. Comparing the results of a nesting study of waterfowl in Canada with the first year's work on the Lower Souris Refuge in North Dakota, Kalmbach (1938: 614) shows that losses of duck nests from the principal predators were about the same on both areas but occurred chiefly through the medium of crows (*Corvus brachyrhynchos*) in the former case and of skunks (*Mephitis*) in the latter; artificial reduction of skunks on the Lower Souris was followed by a greatly lowered loss rate from these animals and a higher total of hatched nests for the second year, but the percentage of loss from factors other than skunks increased in a way that may suggest partial compensation.

Losses of young muskrats from predators (particularly minks, *Mustela vison*), disease, and miscellaneous agencies may be spectacularly heavy, and losses from intraspecific attack may at times equal or exceed the combined mortality from other causes. The Iowa research findings, however, bear out the concept that some of the heaviest losses follow, instead of govern, the directions taken by population curves. Lessening of juvenile mortality from predation and disease tended to be counterbalanced by increased killing of young by older muskrats. Conversely, when predation or disease losses were heavy,

[7] In form corrected for error (Errington, Hamerstrom, and Hamerstrom, 1940: 814).

muskrat intraspecific attacks tended to diminish in proportion.

The aforementioned examples are not listed with intent of introducing confusion into phenomena from which meaning is at best hard enough to extract. Rather, they should warn against placing too much confidence in what may seem obvious or expected.

Correlation of data in a study of productivity admittedly entails tedious work, and the temptation to oversimplify is understandable. Even when there may not be serious hiatuses in the data, it is not always easy to keep in mind just what one may be figuring and why, to be sure just how much one should even attempt to dissociate and appraise the inevitable field variables.

SUMMARY

This paper was prepared to assist students of productivity in avian and mammalian populations to guard against errors arising from neglect of compensatory trends in reproductive and loss rates. Some degree of increased breeding as a result of losses of eggs or of young can be expected for a considerable variety of higher vertebrates, and an analysis of productivity of a hypothetical species (similar in behavior to the ring-necked pheasant) is outlined as an illustration of technique.

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BRIEF CONTRIBUTIONS

Nutrition Experiment with Wild Microtus Populations.—In the course of investigation of fluctuations in animal populations, I have attempted experimental exploration of cyclic phenomena. Conclusions reached from experiments with artificially maintained animals may not legitimately be applied directly to the problems of wild populations. Removal from the wild, in effect, makes a different animal of the subject so far as population phenomena are concerned as they are the resultant of environmental pressure upon the race.

Field experimentation has three manipulations open to it, namely: addition to, subtraction from, and changes in, the environment. First attempts to use field nutrition experimentation in connection with cycle studies were made at Madison, Wisconsin, during the winter and spring of 1936–37. The experiment failed because of the destructive activities of stray dogs. The work was repeated at Pullman, Washington during the winter and spring of 1939–40 and 1940–41. Grass fires in 1940 damaged a large part of the area.

The experimental foods used were head lettuce, yellow corn, carrots, apples, irradiated oat meal, and cod-liver oil. Beginning with the disappearance of snow these were distributed in stations ten to twenty-five yards apart, each containing samples of all the foods. Nothing more was done on the control areas until trapping time.

The results of trapping were as follows:

	Experimental area		Control area	
	1940	1941	1940	1941
Total trap nights	325	238	475	270
Number caught	56[1]	19	20	11
Number per trap-night	.17	.08	0.04	.041
Average weight	27.5[2]	32.7	25.3	24.8
Number of males	15	10	7	6
Males per trap-night	0.05	0.042	0.02	.022
Average weight of males	30.3[3]	30.80[5]	29.4	26.7
Number of females	31	9	13	5
Females per trap-night	0.10	.037	0.03	.023
Average weight of females	25.0[4]	34.4[6]	23.1	23.7

[1] Includes 10 not sexed.
[2] 51 specimens
[3] 14 males
[4] 29 females
[5] 8 males
[6] 4 females

Because of the reduced area available, the samples were unavoidably small. In the spring of 1940, fifty-six *Microtus* specimens were caught during 325 trap-nights on the experimental area while twenty were captured on the control area during 475 trap-nights. As shown by the table, the sex ratio was unbalanced on both areas.

The results of the 1941 trapping were rather meager, presumably because of the exceptionally heavy rains. The sex ratio tended to be nearer equal or even to reverse that of the previous year. The average weight of the animals in the experimental area again exceeded that of the animals on the control area. The weights of the females are probably not representative, varying with pregnancy. The number of mice taken on

both areas was less than the previous year. The difference in the number of animals caught may be inherent in the areas or may perhaps be the result of the better nutrition. It is likely that the consistently higher average weight on the experimental areas was the result of the addition of nutrients.—LEONARD WING, State College of Washington, Pullman, Washington.

NOTE

There is demand for information as to current wildlife research being conducted throughout the United States. In order to supply this, the U. S. Fish and Wildlife Service will endeavor to assemble and release annually a statement on the subject. It is therefore suggested that any interested person send before June 1, 1942, to the Fish and Wildlife Service, U. S. Department of the Interior, Washington, D. C., titles of research problems upon which he may be working, with the year of probable completion, and his name and address.